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REVISION OF THE WOLF SPIDERS OF THE GENUS *ARCTOSA* C. L. KOCH IN NORTH AND CENTRAL AMERICA (ARANEAE:LYCOSIDAE)

Charles D. Dondale and James H. Redner

Biosystematics Research Institute
Research Branch, Agriculture Canada
Ottawa, Ontario K1A 0C6

ABSTRACT

The genus *Arctosa* C. L. Koch, 1848 (= *Arkalosula* Roewer, 1960, new synonym) is revised for North and Central America. Twelve species are described or redescribed, illustrated, keyed, and mapped: *A. raptor* (Kulczynski, 1885), new combination (= *Lycosa quinarya* Emerton, 1894, new synonym); *A. emertoni* Gertsch, 1934; *A. rubicunda* (Keyserling, 1877) (= *A. imperiosa* Gertsch, 1933, new synonym); *A. virgo* (Chamberlin, 1925); *A. lama*, new species; *A. alpigena* (Doleschall, 1852); *A. insignita* (Thorell, 1872); *A. perita* (Latreille, 1799); *A. minuta* F. Pickard-Cambridge, 1902 (= *A. cheluncata* Petrunkevitch, 1925, new synonym); *A. sanctaerosae* Gertsch and Wallace, 1935; *A. littoralis* (Hentz, 1844) (= *A. trifida* F. Pickard-Cambridge, 1902 and *A. panamana* Petrunkevitch, 1925, new synonyms); *A. serii* Roth and Brown, 1976.

INTRODUCTION

Wolf spiders of the genus *Arctosa* are of medium to large size, with overall length (excluding legs) of 4.5 - 16.0 mm. They are swift runners, and possess relatively keen eyesight. Most dwell in sandy places such as seashores or the banks of rivers and lakes, though some occupy heath or lichen habitats in high mountains or arctic tundra. The principal body colors are gray, off-white, and tawny brown, in keeping with habitat. Females usually attend their eggs in silk-lined burrows rather than carry them about, and most species appear to be nocturnal. Two members of the genus, *A. variana* C. L. Koch and *A. perita* (Latreille), have achieved notability for their skill in returning to the home stream bank when carried some distance away on water; they appear to orient themselves by means of the sun's (or moon's) position in the sky and of an internal clock (Papi and Tongiorgi 1963, Tongiorgi 1970).

The genus *Arctosa* was established by C. L. Koch (1848) for 10 species of European wolf spiders. Some 70 world species were recorded as of 1939 (Bonnet 1955), though a current estimate is about 50 species. Gertsch (1934) reviewed the North American species, and Lugetti and Tongiorgi (1965, 1966) reviewed the central European species.

The 12 North and Central American species of *Arctosa* are here revised. Methods and terminology are those given by Dondale and Redner (1978, 1979). The male palpus and the epigynum of the type-species, *A. cinerea* (Fabricius), are illustrated (Figs. 1-4) for comparison with New World representatives.

Tessarops maritimus Rafinesque, 1821 is unknown to us, and we therefore treat the name as a *nomen dubium*. The species was so vaguely described that we cannot be sure even that it is a spider. Bonnet (1959: 4312) tentatively classified it as a gnaphosid, whereas Kaston (1972) speculated that it is the wolf spider *Arctosa littoralis* (Hentz, 1844). We agree with Kaston that *T. maritimus* may represent an anomalous specimen of *littoralis*, but we also agree that "in the interests of nomenclatorial stability the well known name [*littoralis*] should be retained, . . ."

The group of species exemplified by *Arctosa funera* (Hentz), previously included in *Arctosa*, will be treated separately under the genus *Allocosa* Banks, 1904.

Abbreviations used in the text of this paper for names of lending institutions are explained in the acknowledgments. Measurements are given as the means and standard deviations for samples of ten or more specimens, or as ranges for less than ten.

ARCTOSA C. L. KOCH

Lycosa: C. L. Koch 1837:23 (in part); Chamberlin 1908:220 (in part); Simon 1937:1089 (6th Group).

Arctosa C. L. Koch, 1848:94; Simon 1898:328 (in part, as subgenus of *Lycosa*); 1937:1089 (9th Group); Dahl and Dahl 1927:65 (in part); Petrunkevitch 1928:104 (in part); Gertsch 1934:3 (in part); Holm 1947:19; Kaston 1948:318 (in part); 1978:188; Locket and Millidge 1951:283; Bonnet 1955:640 (in part); Roewer 1955:225 (in part); 1960:591 (in part); Wiebes 1959:26 (in part); Lugetti and Tongiorgi 1965:167; 1966:134; Fuhn and Niculescu - Burlacu 1971:173.

Tricca Simon, 1889:250 (in part, including type-species); Roewer 1955:297 (in part); 1960:950; Bonnet 1959:4684 (in part); Braun 1963:81 (in part); Lugetti and Tongiorgi 1965:209 (in part); 1966:144 (in part).

Allocosa: Roewer 1955:201 (in part).

Crocodilosa: Roewer 1955:238 (in part); 1960:847 (in part).

Arctosella Roewer, 1960:671 (in part, including type-species). Synonymized by Guy 1966:48.

Arkalosula Roewer, 1960:759 (in part, including type-species). Validation of generic name originally proposed without statement of characters by Roewer 1955:231. NEW SYNONYM.

Trochosomma Roewer, 1960:851 (in part, not including type-species).

Citilycosa Roewer, 1960:845 (in part, not including type-species).

Type-species.—Of *Arctosa*, *Aranea cinerea* Fabricius, 1777 by subsequent designation (Simon 1937:1089). Of *Tricca*, *Tricca japonica* Simon, 1899 by original designation. Of *Arctosella*, *Aranea perita* Latreille, 1799 by original designation. Of *Arkalosula*, *Arctosa sanctaerosae* Gertsch and Wallace, 1935 by original designation.

Description.—Size medium to large (overall length, excluding legs, 4.5 - 16.0 mm). Carapace broad, rather low, approximately uniform in height between dorsal groove and posterior row of eyes, usually glabrous or nearly so, yellow, off-white, or mottled with gray, yellow, or brown. Anterior row of eyes straight or somewhat procurved or recurved, longer than, shorter than, or equal to middle row in length. Promargin of fang furrow with two or three teeth, and retromargin with three teeth. Legs usually pale, robust, lightly scopulate, with dark rings; tibia III with two dorsal macrosetae or with one plus a basal bristle, and with 1-3 retrolateral macrosetae; trochanters usually deeply notched at tip on ventral surface. Abdomen usually pale and mottled like carapace. Terminal apophysis of male palpus (Fig. 9) conspicuous, in two parts or in one part of two different shapes and degrees of sclerotization; embolus (Figs. 7, 9) straight or curved, largely hidden by median apophysis in ventral view, with extensive pars pendula extending nearly to tip; median apophysis (Figs. 7, 9) prominent, sclerotized, elongate, conspicuously

grooved or excavated on distal or dorsal surface (and forming part of functional conductor); tegulum (Fig. 9) with retrolateral prominence bearing small soft area and often bearing small, transparent, cup-shaped process or prominent, sclerotized process, which also form part of functional conductor. Epigynum of female usually with conspicuous atrium divided by median septum, without hood (Figs. 3, 5); copulatory openings located at sides of slender part of median septum; copulatory tubes (Figs. 4, 32) slender to stout, rather short, often curved or sinuous (Fig. 32), sometimes with conspicuous spermathecal organs at lateral margins; spermathecae (Fig. 6) bulbous in outline, without prominences.

Diagnosis.-*Arctosa* is grouped with *Lycosa*, *Schizocosa*, *Geolycosa*, *Alopecosa*, and *Trochosa*, in which the conductor (the structure in which lies the resting embolus of the male palpus) is a secondary one derived partly of a groove or excavation on the distal or dorsal surface of the median apophysis and partly of a process on the retrolateral margin of the tegulum. The members *Arctosa* differ from those of the other genera by having the terminal apophysis neither long and sickle-shaped (compare *Lycosa*, *Geolycosa*, *Trochosa*) nor minute and scale like (compare *Schizocosa*) but prominent and usually in two parts with differing degrees of sclerotization (Fig. 9). In addition, the process on the tegulum in *Arctosa* is usually inconspicuous and often concealed (ventral view) by the median apophysis and is only observable by dissection. The mottled body, rather low, glabrous carapace, and the lack of an epigynal hood also have diagnostic value for *Arctosa*.

The presence of a dorsal bristle on distitarsus I, used by some authors to distinguish *Arctosa*, is subject to exception, and the character is also found in representatives of other lycosid genera. The same comments apply to the replacement of the dorsal basal macroseta on tibia III and IV by a bristle.

Comments.-Simon (1889) described the genus *Tricca* for *T. japonica* Simon (the type-species) together with *T. lutetiana* (Simon). The characters on which he established the genus were the exaggerated length of the anterior row of eyes, the recurvature of the same row, and the reduction of macrosetae on legs I and II. Our study of specimens of *T. japonica* (and of all Holarctic species of *Arctosa*) indicates that none of these characters differentiates *Tricca* from *Arctosa*. Moreover, the external genitalia show no significant difference between the two genera. We therefore regard *Tricca* as a junior synonym of *Arctosa*. The status of the European *lutetiana*, however, remains uncertain.

The genera *Arctosella* and *Arkalosula* were established by Roewer (1960) with type-species that we regard as belonging to *Arctosa*.

KEY TO NORTH AND CENTRAL AMERICAN
SPECIES OF *ARCTOSA*

- 1. Carapace uniformly dark, and more than 3.0 mm in width. Male palpus with angular, flat median apophysis (Fig. 7). Median septum of epigynum with transverse piece elongate (Fig. 5) *raptor* (Kulczynski)
- Carapace pale (at least in part) or, if uniformly dark, then less than 3.0 mm in width. Male palpus with median apophysis variously shaped but not angular and flat. Median septum of epigynum with transverse piece, if developed, usually short and stout 2

2. Anterior row of eyes distinctly longer than middle row (as in Fig. 8). 3
Anterior row of eyes not longer than middle row (Figs. 31, 65) 4
3. Legs with dark rings. *emertoni* Gertsch
Legs without dark rings *rubicunda* (Keyserling)
4. Carapace uniformly dark. Anterior row of eyes shorter than middle row (Fig. 31).
Femur I with two dorsal macrosetae 5
Carapace pale (at least in part). Anterior row of eyes approximately as long as
middle row (Fig. 65). Femur I usually with three dorsal macrosetae 6
5. Male palpus with short, rotund median apophysis (Fig. 22). Spermathecae attached
mesally to copulatory tubes (Figs. 25, 26) *virgo* (Chamberlin)
Male palpus with elongate median apophysis (Fig. 29). Spermathecae attached la-
terally to copulatory tubes (Fig. 32) *lama* new species
6. Abdominal heart mark densely covered with compound setae (Fig. 37). Pale median
area of carapace narrow posteriorly, gradually widening anterior to dorsal groove
(Fig. 40) 7
Abdominal heart mark sparsely covered with simple setae (Fig. 41). Pale median
area of carapace widest at level of dorsal groove (Fig. 66), or carapace entirely pale
. 8
7. Male palpus in retrolateral view with tip of median apophysis distinctly hooked
(Fig. 38). Epigynum with broad transverse septum (Figs. 33, 34)
. *alpigena* (Doleschall)
Male palpus in retrolateral view with tip of median apophysis straight (Fig. 44).
Epigynum with triangular septum (Fig. 42) *insignita* (Thorell)
8. Sternum dark brown or black. Tibia and basitarsus I lacking retrolateral macrosetae
(exclusive of any at tip). Anterior median eyes slightly larger than anterior lateral
eyes *perita* (Latreille)
Sternum yellow, orange, or orange brown. Tibia and basitarsus I with one or more
retrolateral macrosetae (exclusive of any at tip). Anterior median eyes distinctly
larger than anterior lateral eyes (Fig. 65) 9
9. Tibia III with two dorsal macrosetae *minuta* F. Pickard-Cambridge
Tibia III with one dorsal macroseta plus a basal bristle 10
10. Promargin of cheliceral fang furrow with three teeth. Tibia I with one dorsal
macroseta *sanctaerosae* Gertsch and Wallace
Promargin of cheliceral fang furrow with two teeth. Tibia I without dorsal macro-
setae 11

11. Femur I with two prolateral macrosetae near tip. Tibia III with three retrolateral macrosetae. Legs usually with dark rings *littoralis* (Hentz)
- Femur I with one prolateral macroseta near tip. Tibia III with two retrolateral macrosetae. Legs without dark rings *serii* Roth and Brown

Arctosa raptor (Kulczynski), new combination
Figs. 5-8; Map 1

Pirata raptor Kulczynski, 1885:55, Pl. 11, fig. 61; Schenkel 1930:32, fig. 13; Sytschewskaia 1935:83; Bonnet 1958:3671.

Lycosa quinaria Emerton, 1894:422, Pl. 3, figs. 5, 5a; 1911:400, figs. 1, 1a; 1915:160; 1920:328; Chamberlin 1908:277, Pl. 19, fig. 7. NEW SYNONYM.

Tarentula raptor: Strand 1906:468.

Arctosa quinaria: Gertsch 1934:5; Chamberlin and Ivie 1947:18, Pl. 2, fig. 10; Hackman 1954:77; Bonnet 1955:659; Roewer 1955:231.

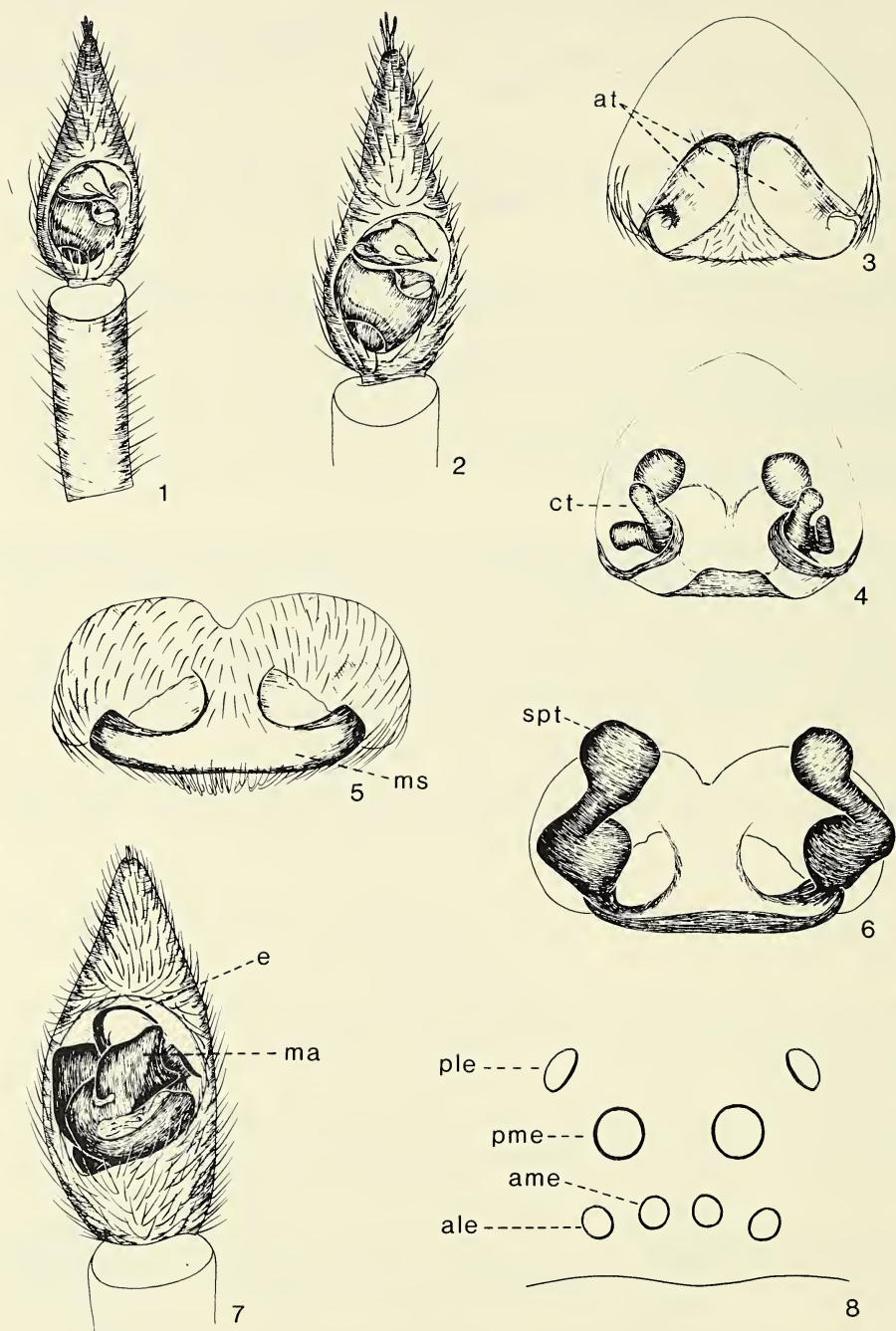
Trochosa raptor: Roewer 1955:299.

Type data.—Female holotype of *raptor* from Petropavlovsk, Kamtchatka (B. Dybowski), in Polish Academy of Sciences, Warsaw, examined. Female holotype of *quinaria* from Lake Louise (“Laggan”), Alberta (Bean), in the MCZ, examined.

Male.—Total length 8.0 - 11.7 mm. Carapace 4.97 ± 0.32 mm long and 3.71 ± 0.26 mm wide; ratio of carapace width to basitarsus IV length 0.63 - 0.77 (20 specimens). Carapace red brown, covered with black setae. Anterior row of eyes procurved, approximately as long as middle row, with eyes uniform in size and spacing. Chelicerae red brown; promargin of fang furrow with three teeth. Legs red brown, without dark rings, with dense scopulae; femur I with three dorsal macrosetae, one or two prolaterals; tibia I with one



Map 1.—Geographical distribution of *Arctosa raptor* (Kulczynski).



Figs. 1-8.—Structures of *Arctosa* spp.: 1-4, *A. cinerea* (Fabricius); 1, 2, palpi of male, ventral view; 3, epigynum; 4, spermathecae; 5-8, *A. raptor* (Kulczynski); 5, epigynum; 6, spermathecae; 7, palpus of male, ventral view; 8, eyes, frontal view. *ale*, anterior lateral eye; *ame*, anterior median eye; *at*, atrium; *ct*, copulatory tube; *e*, embolus; *ma*, median apophysis; *ms*, median septum; *ple*, posterior lateral eye; *pme*, posterior median eye; *spt*, spermatheca.

dorsal macroseta, two prolaterals, two retrolaterals; basitarsus I with none or one prolateral macroseta (exclusive of any at tip), none or one retrolateral (exclusive of any tip); tibia III with one or two dorsal macrosetae. Abdomen dusky, with off-white heart mark and a few off-white chevrons; heart mark covered with compound setae. Terminal apophysis of palpus minute; embolus short, curved; median apophysis (Fig. 7) large, angular, flat, with broad excavation on dorsal surface.

Female.—Total length 11.0 - 16.0 mm. Carapace 5.59 ± 0.54 mm long and 4.32 ± 0.52 mm wide; ratio of carapace width to basitarsus IV length 0.81 - 0.90 (20 specimens). General structure and color essentially as in male, but anterior row of eyes usually longer than middle row (Fig. 8), tibia I lacking dorsal and retrolateral macrosetae, and tibia III with basal dorsal macroseta replaced by bristle. Epigynum with short, broad, flat median septum having elongate transverse piece (Fig. 5). Copulatory tubes stout; spermathecae bulbous (Fig. 6).

Diagnosis.—Specimens of *A. raptor* differ from those of other species in the genus by the large size in combination with a uniformly dark carapace having black setae, by the dense leg scopulae, by the minute terminal apophysis and angular, flat median apophysis of the male palpus, and by the elongate, transverse piece of the median septum.

Range.—Alaska to Newfoundland, south to Maine; U.S.S.R.

Natural history.—*A. raptor* is an inhabitant of bogs, river banks, wet meadows, and dense coniferous forests (Hackman 1954). Sytschewskaia (1935) found females in burrows at water's edge in sphagnum bogs. A male and female were taken together by the authors on alpine tundra at the summit of Mont Albert, Gaspé Peninsula, Québec. Adults have been collected from June 5 to September 12.

Arctosa emertoni Gertsch

Figs. 9-15; Map 2

Lycosa polita Emerton, 1885:484 (in part, Pl. 46, fig. 2a, not lectotype—see *A. rubicunda*); 1902:70 (in part, fig. 171).

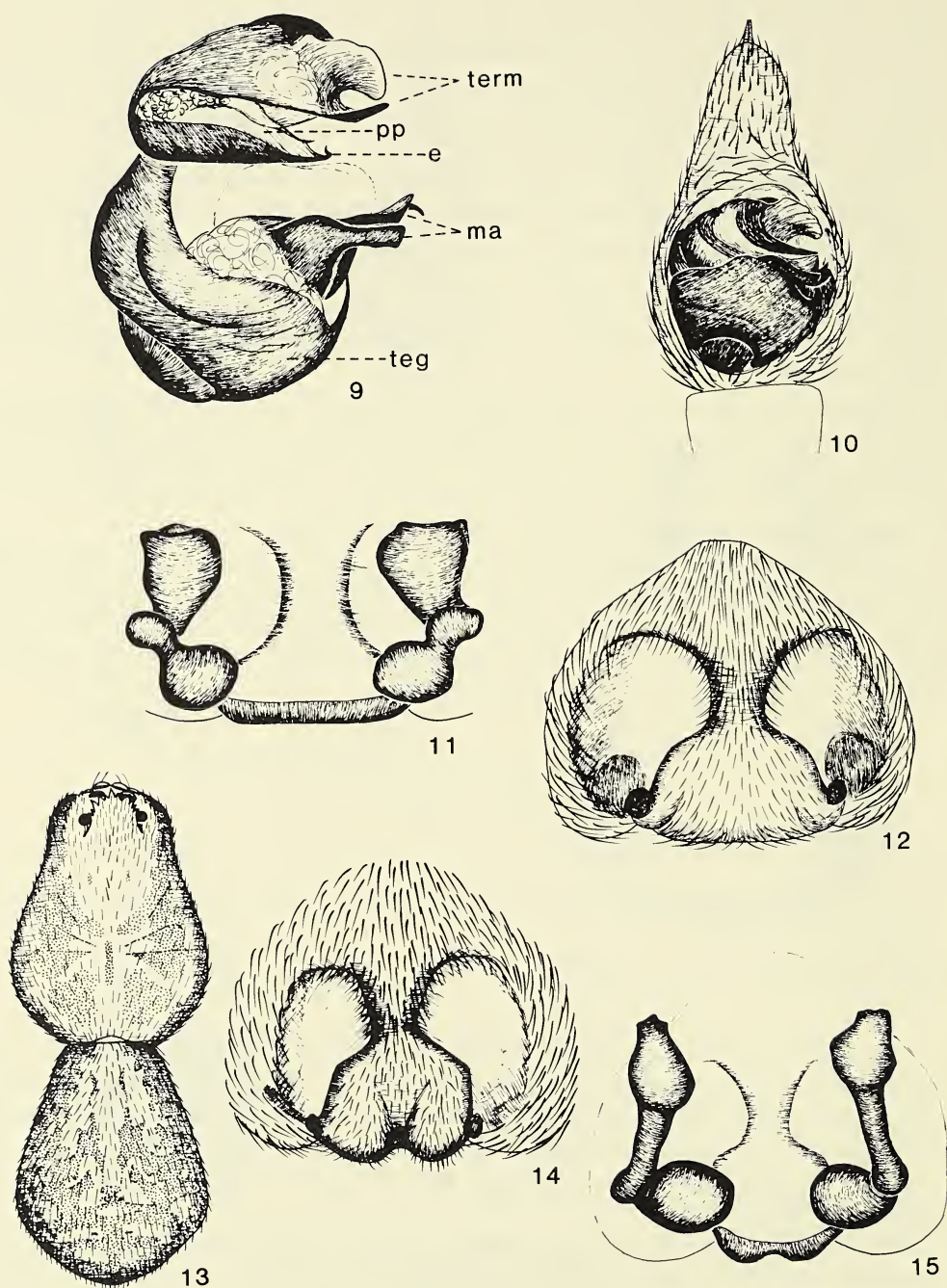
Arctosa emertoni Gertsch, 1934:5; Kaston 1948:319, Pl. 53, figs. 1047-1049; Levi and Field 1954:455; Bonnet 1955:647.

Crocodylosa emertoni: Roewer 1955:238.

Trochosomma emertoni: Roewer 1960:851.

Type data.—Female from Albany, New York, February 1871 (J. H. Emerton), and female from Arlington Heights, Massachusetts, April 26 1877 (J. H. Emerton) (among specimens of mixed syntype-series of J. H. Emerton, but not lectotype or paralectotypes of *polita*—see *A. rubicunda*), in MCZ, examined. Male holotype and female allotype of *emertoni* from Wacouta Beach, Lake Pepin, Minnesota, May 15 1932 (W. J. Gertsch), in AMNH, examined.

Male.—Total length 6.4 - 9.9 mm. Carapace 4.18 ± 0.41 mm long and 3.06 ± 0.29 mm wide; ratio of carapace width to basitarsus IV length 0.47 - 0.54 (20 specimens). Carapace red brown, mottled laterally with pale spots, paler mesally, darker near eyes, glistening, nearly glabrous (as in fig. 13). Anterior row of eyes straight or slightly recurved, distinctly longer than middle row, with median eyes larger than lateral eyes. Chelicerae red brown; promargin of fang furrow with three teeth. Sternum pale. Legs straw yellow to pale brown, with dark rings on femora and tibiae, with sparse scopulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, one prolateral, no retrolaterals; basitarsus I with none to 2 prolateral macrosetae (exclusive of any



Figs. 9-15.—Structures of *Arctosa emertoni* Gertsch: 9, expanded bulb of male palpus, ventral view; 10, palpus of male, ventral view; 11, 15, spermathecae; 12, 14, epigyna; 13, body of female, dorsal view. *e*, embolus; *ma*, median apophysis; *pp*, pars pendula; *teg*, tegulum; *term*, terminal apophysis.

at tip), none or one retrolateral (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen dark brown, mottled extensively with off-white; venter pale. Terminal apophysis of palpus with broad distal part and slender basal part; embolus nearly straight; median apophysis prominent, somewhat curved (ventral view), with stout curved process at tip (Figs. 9, 10).

Female.—Total length 6.9 - 12.0 mm. Carapace 4.44 ± 0.40 mm long and 3.29 ± 0.30 mm wide; ratio of carapace width to basitarsus IV length 0.96 - 1.12 (20 specimens). General structure and color essentially as in male, but tibia I with two prolateral macrosetae. Epigynum with median septum gradually widening posteriad (Figs. 12, 14). Spermathecae bulbous (Figs. 11, 15).

Diagnosis.—Specimens of *A. emertoni* most resemble those of *A. rubicunda* in that the anterior row of eyes is distinctly longer than the middle row; they can be distinguished from *rubicunda* by the possession of dark rings on the legs, by the more distinctly mottled carapace, and by the curved median apophysis (ventral view) of the male palpus.

Range.—Interior British Columbia to Nova Scotia, south to Utah, Colorado, and North Carolina.

Natural history.—*A. emertoni* has been found in shady woodlands and grasslands, and occasionally on bogs or seashores. Adults have been collected from April 5 to October 28.



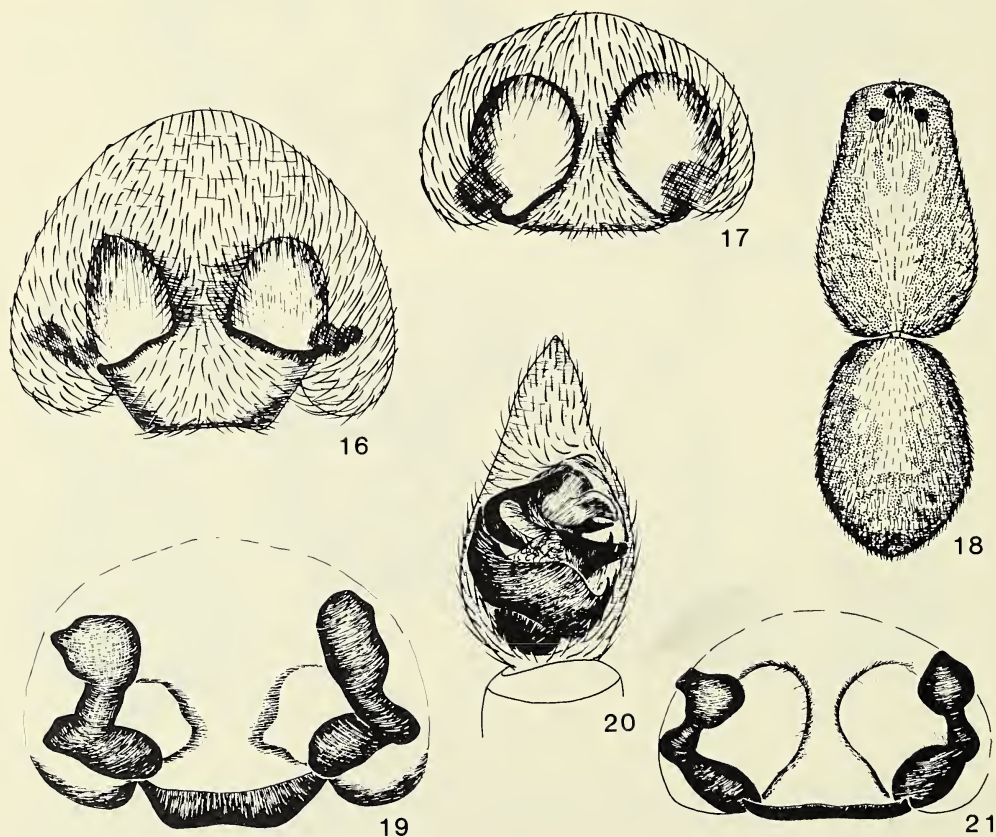
Map 2.—Geographical distribution of *Arctosa emertoni* Gertsch.

Arctosa rubicunda (Keyserling)

Figs. 16-21; Map 3

Trochosa rubicunda Keyserling, 1877: 663, Pl. 8, fig. 40; Montgomery 1904: 307, Pl. 20, fig. 30.*Lycosa polita* Emerton, 1885:484 (in part, Pl. 46, figs. 2, 2b, 2c).*Lycosa rubicunda*: Simon 1898:33; Chamberlin 1908:278, Pl. 19, fig. 9; Comstock 1940:656.*Arctosa rubicunda*: Petrunkevitch 1911:552; Gertsch 1934:5; Kaston 1948:319, Pl. 53, figs. 1044 - 1046; 1978:188, fig. 480; Levi and Field 1954:455; Bonnet 1955:660.*Arctosa imperiosa* Gertsch, 1933:13, fig. 17, 1934:5; Bonnet 1955:649. NEW SYNONYM.*Crocodilosa rubicunda*: Roewer 1955:238.*Crocodilosa imperiosa*: Roewer 1955:238; 1960:847.

Type data.—Female holotype of *rubicunda* from Baltimore, Maryland, not located; identified from original description and illustration. Female lectotype and one female paralectotype of *polita* from Blue Hills, Boston, Massachusetts, May 18 1877 (J. H. Emerton), in MCZ, examined and here designated; the specimens bear our lectotype and paralectotype labels, respectively. Female paralectotype of *polita* from Albany, New York, February 1871 (J. H. Emerton), in MCZ, examined and here designated; the specimen bears our paralectotype label. Female holotype of *imperiosa* from Colorado Springs, Colorado, July 20 1908, in AMNH, examined.



Figs. 16-21.—Structures of *Arctosa rubicunda* (Keyserling): 16, 17, epigyna; 18, body of female, dorsal view; 19, 21, spermathecae; 20, palpus of male, ventral view.

Male.—Total length 6.6 - 9.3 mm. Carapace 4.24 ± 0.34 mm long and 2.92 ± 0.24 mm wide; ratio of carapace width to basitarsus IV length 0.85 - 1.01 (20 specimens). Carapace dark red brown, with tan median area and with indistinct paler mottling laterally, glistening, nearly glabrous (as in fig. 18). Anterior row of eyes straight, longer than middle row, with median eyes larger than lateral eyes. Chelicerae dark red brown; promargin of fang furrow with three teeth. Sternum pale red brown. Legs red brown, without dark rings, with sparse scopulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, two prolaterals, no retrolaterals; basitarsus I with 2 prolateral macrosetae (exclusive of any at tip), none or one retrolateral (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen dark brown, mottled, with indistinct heart mark and chevrons; venter pale. Terminal apophysis of palpus with large distal part and slender basal part (Fig. 20); embolus nearly straight; median apophysis long, prominent, nearly straight (ventral view), with stout process at tip (Fig. 20).

Female.—Total length 8.0 - 12.0 mm. Carapace 4.77 ± 0.49 mm long and 3.40 ± 0.39 mm wide; ratio of carapace width to basitarsus IV length 1.00 - 1.14 (20 specimens).



Map 3.—Geographical distribution of *Arctosa rubicunda* (Keyserling).

General structure and color essentially as in male. Epigynum with median septum gradually widening posteriad (Figs. 16, 17). Spermathecae bulbous (Figs. 19, 21).

Diagnosis.—Specimens of *A. rubicunda* most resemble those of *A. emertoni*, both having the anterior row of eyes longer than the middle row; they can be distinguished from the latter by the lack of dark rings on the legs, by the nearly uniform coloring of the carapace, and by the straight median apophysis of the male palpus (ventral view).

Gertsch (1933) described *A. imperiosa* from Colorado; the body size and external genitalia are consistent with these characters in *A. rubicunda*, but the color of carapace and legs is intermediate between *rubicunda* and *emertoni*. Twelve specimens, including both males and females and collected in Nebraska, North Dakota, Montana, Saskatchewan, and western Wisconsin, have been identified as this intermediate form. We are reluctant to accept *imperiosa* as a valid species in the absence of supporting data from behavior, habitat relations, or life history.

Range.—Western Northwest Territories to Nova Scotia, south to Colorado, Kansas, and southern Pennsylvania.

Natural history.—Specimens of *A. rubicunda* have been collected in bogs, meadows, fields, prairies, and deciduous forests, and also at the margins of ponds and salt marshes, and on beaches. Adults were collected from May 20 to October 3. Kaston (1948) records eggs in June and July.

Arctosa virgo (Chamberlin)

Figs. 22-26, 28; Map 4

Allocosa virgo Chamberlin, 1925:226; Roewer 1955:201.

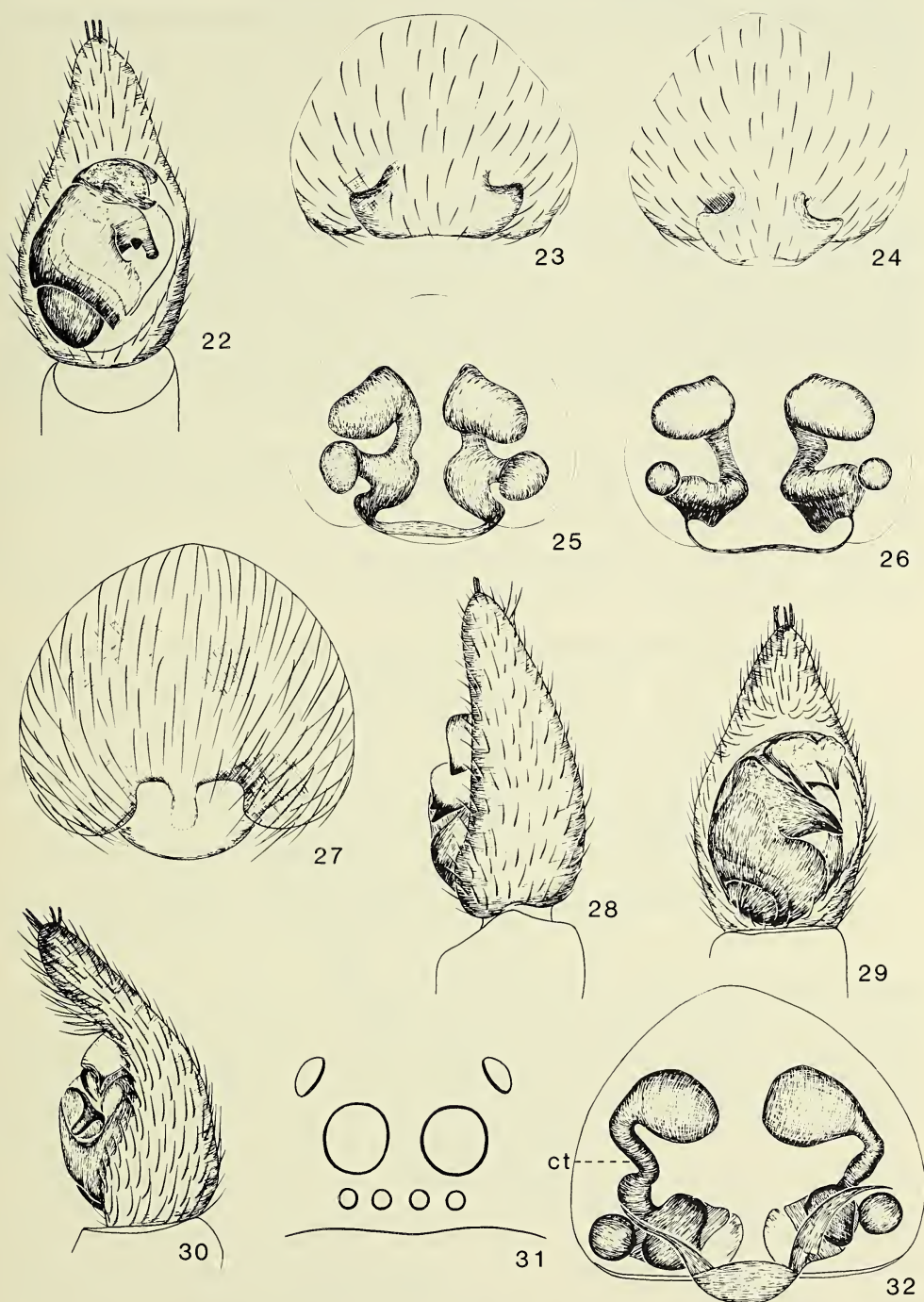
Arctosa virgo: Gertsch 1934:7; Kaston 1948:320, Pl. 53, figs. 1051, 1052, Pl. 54, fig. 1053; Bonnet 1955:662.

Type data.—Female holotype and one female paratype from Fairfax, Virginia (R. V. Chamberlin), in MCZ, examined.

Male.—Total length 5.1 - 6.9 mm. Carapace 2.81, 3.32 mm long and 2.04, 2.47 mm wide (2 specimens). Carapace red brown, without pale band or spots. Anterior row of eyes straight to procurved, shorter than middle row, with eyes uniform in size (as in fig. 31). Chelicerae red brown; promargin of fang furrow with two or three teeth. Sternum pale. Legs red brown, with femora and tibiae faintly ringed; femur I with two dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, two prolaterals, no retrolaterals; basitarsus I with 1-3 prolateral macrosetae (exclusive of any at tip), no retrolaterals (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen dusky or charcoal gray, with pale yellow heart mark and small paired yellow spots along dorsum; venter pale, with broad dusky longitudinal band. Terminal apophysis of palpus in two parts; embolus short, curved; median apophysis short, rotund (Fig. 22).

Female.—Total length 5.0 - 6.6 mm. Carapace 2.93 ± 0.24 mm long and 2.11 ± 0.21 mm wide (13 specimens). General structure and color essentially as in male. Epigynum with inconspicuous median septum (Figs. 23, 24). Copulatory tubes slender; spermathecae elongate, attached mesally to copulatory tubes (Figs. 25, 26).

Diagnosis.—Specimens of *A. virgo* most resemble those of *A. lama* but are distinguished from the latter by the short, rotund median apophysis of the male palpus and by the mesal attachment of the spermathecae to the copulatory tubes.



Figs. 22-32.—Structures of *Arctosa* spp.: 22-26, 28, *A. virgo* (Chamberlin); 22, 28, palpi of male, 22, ventral view, 28, retrolateral view; 23, 24, epigyna; 25, 26, spermathecae; 27, 29-32, *A. lama* new species; 27, epigynum; 29, 30, palpi of male, 29, ventral view, 30, retrolateral view; 31, eyes, frontal view; 32, spermathecae. *ct*, copulatory tube.

Range.—Southern Michigan to New Jersey, south to Tennessee.

Natural history.—The habitat of *A. virgo* is unknown to us. Adults were collected from May to early August.

Arctosa lama, new species

Figs. 27, 29-32; Map 4

Type data.—Male holotype from Mer Bleue bog, east of Ottawa, Carleton Co., Ont., June 18 1974 (J. H. Redner and C. D. Dondale), in CNC; 27 male and four female paratypes from the type locality, in CNC; 14 male and two female paratypes from Upper Rock Lake, near Chaffey's Locks, Ontario, in CNC; 10 male and seven female paratypes from Kouchibouguac National Park, New Brunswick, in CNC; one female paratype from Lockeport, Nova Scotia, in CNC; one male and two female paratypes from Bethany, Connecticut, in AMNH; 1 female paratype from 4.5 miles east of Gorda, Tuscaloosa County, Alabama, in CNC.

Male.—Total length 4.5 - 5.3 mm. Carapace 2.81 ± 0.14 mm long and 1.98 ± 0.12 mm wide (20 specimens). Carapace red brown, with few short dark setae. Anterior row of eyes straight to procurved, shorter than middle row, with eyes uniform in size (Fig. 31). Chelicerae red brown; promargin of fang furrow with two or three teeth. Sternum pale red brown. Legs red brown, darker distally, without rings, with sparse scopulae; femur I



Map 4.—Geographical distribution of *Arctosa* spp.: *A. virgo* (Chamberlin), circles; *A. lama* new species, stars.

with two dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, one or two prolaterals, no retrolaterals; basitarsus I with two or three prolateral macrosetae (exclusive of any at tip), none or one retrolateral (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen dusky, with pale heart mark and with irregular pale spots laterally; venter pale yellow brown. Terminal apophysis of palpus small, fingerlike (Fig. 29); embolus short, curved; median apophysis elongate, curved (Figs. 29, 30).

Female.—Total length 4.8 - 6.4 mm. Carapace 2.81 ± 0.14 mm long and 1.97 ± 0.12 mm wide (19 specimens). General structure and color essentially as in male. Epigynum with indistinct median septum (Fig. 27). Copulatory tubes slender; spermathecae bulbous, attached laterally to copulatory tubes (Fig. 32).

Diagnosis.—Specimens of *A. lama* most resemble those of *A. virgo* but can be distinguished from the latter by the elongate median apophysis of the male palpus and by the lateral attachment of the spermathecae to the copulatory tubes.

Range.—Ontario to Nova Scotia, south to Alabama.

Natural history.—All specimens of *A. lama* for which habitat data are available were collected on sphagnum bogs. Adults were collected from May 25 to August 29.

Arctosa alpigena (Doleschall)

Figs. 33-41; Map 5

Lycosa alpigena Doleschall, 1852:643; Simon 1937: 1112, 1138, figs. 1745, 1746 (in part).

Lycosa superba L. Koch, 1872:316.

Lycosa biunguiculata O. Pickard-Cambridge, 1873:526, Pl. 46, fig. 2.

Lycosa albohastata Emerton, 1894:423, Pl. 3, fig. 3; Chamberlin 1908:275, Pl. 19, fig. 1; Roewer 1955:231.

Arctosa alpigena: Dahl 1908:307, fig. 37; Dahl and Dahl 1927:67, figs. 174-176; Gertsch 1934:4; Braendegaard 1939:6, figs. 2, 4, 5; 1946:10; Palmgren 1939:73, figs. 122-124; Gertsch and Jellison 1939:3; Holm 1947:22, Pl. 4, figs. 46, 47, Pl. 9, fig. 22; Levi and Levi 1951:223, figs. 9, 20; Locket and Millidge 1951:286, figs. 137A, 138E; Hackman 1954:78; Tyschenko 1971:172, figs. 516, 523; Bonnet 1955:641; Roewer 1955:227.

Tricca alpigena: Lugetti and Tongiorgi 1965:212, Pl. 16, figs. 1-3; 1966:145, fig IV (5, 7).

Citilycosa alpigena: Roewer 1960:845.

Type data.—Syntypes of *alpigena* from "Ochsenboden des Schneeberges", Austria (Mann), not located; species identified from original description and from subsequent published descriptions. Nine male, 12 female, and 21 juvenile syntypes of *superba* from Austrian Alps, in BMNH, examined. Male holotype of *biunguiculata* from Braemar, Scotland, not located. One male and one female syntype of *albohastata* from Lake Louise ("Laggen"), Alberta (J. H. Emerton), in MCZ, examined.

Male.—Total length 4.8-6.4 mm. Carapace 3.34 ± 0.22 mm long and 2.45 ± 0.15 mm wide (20 specimens). Carapace dark red brown, with pale median area gradually widening anterior to dorsal groove (as in fig. 40), with few short pale setae. Anterior row of eyes slightly procurved, nearly as long as middle row, with eyes approximately uniform in size. Chelicerae dark red brown; promargin of fang furrow with three teeth. Sternum dark red brown to black. Legs pale red brown, usually with dark rings on femora and tibiae, with sparse scopulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, two prolaterals, two retrolaterals; basitarsus I with two or three prolateral macrosetae (exclusive of any at tip), 0-3 retrolaterals (exclusive of any at tip);

tibia III with one dorsal macroseta plus a basal bristle. Abdomen red brown, with dark brown or black reticulations; heart mark white, densely covered with compound setae. (Fig. 37). Terminal apophysis of palpus with soft distal part and slender, hard basal part (Fig. 35); embolus long, slender, sinuous; median apophysis broad, drawn out to fine hooked tip (Figs. 35, 38).

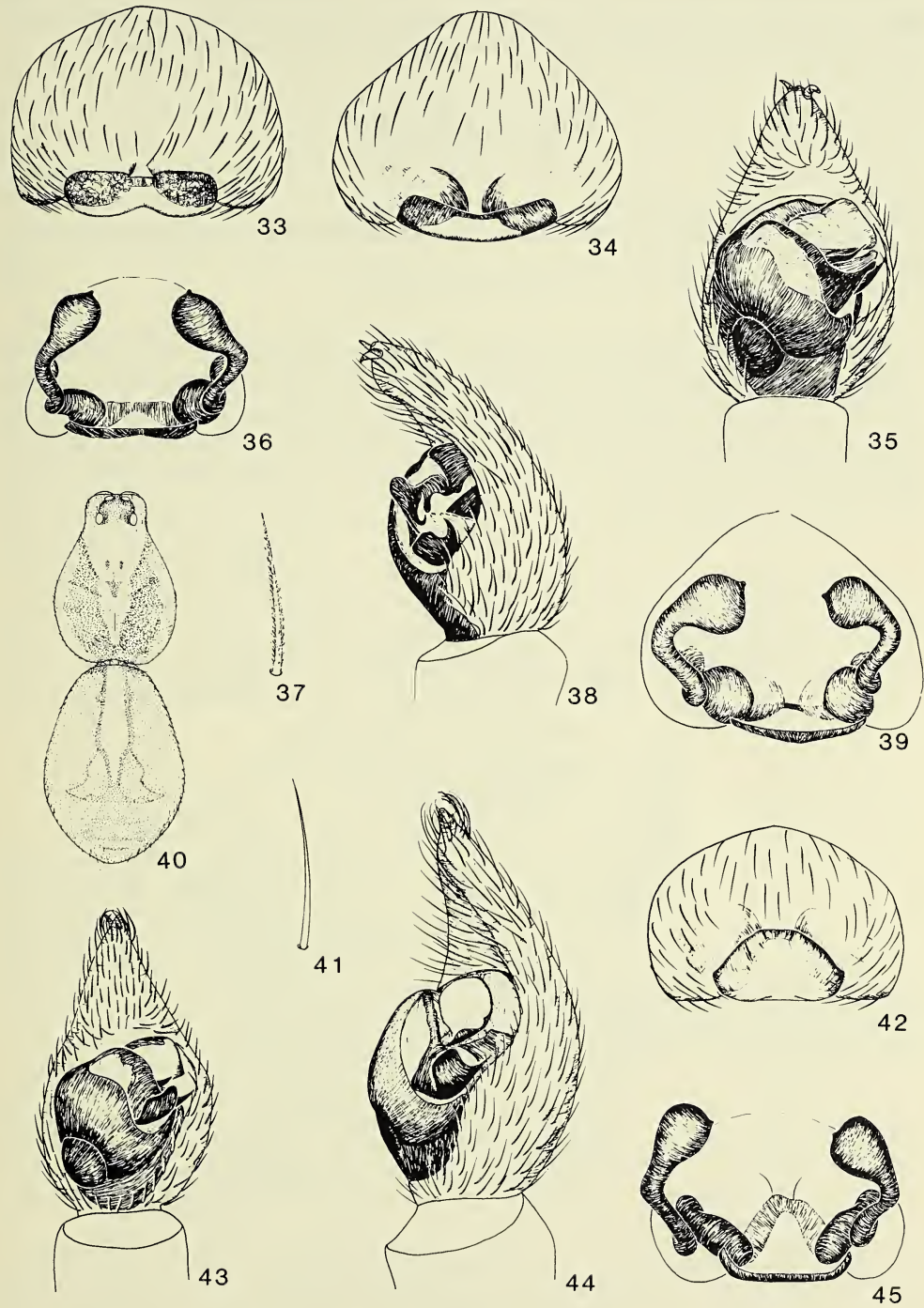
Female.—Total length 6.7-9.3 mm. Carapace 3.65 ± 0.25 mm long and 2.71 ± 0.20 mm wide (20 specimens). General structure and color essentially as in male, but tibia I with one or two prolateral macrosetae and none or one retrolateral macroseta. Epigynum with median septum broad, transverse (Figs. 33, 34). Copulatory tubes slender, curved or slightly sinuous; spermathecae bulbous (Figs. 36, 39).

Diagnosis.—Specimens of *A. alpigena* most resemble those of *A. insignita*, being similar in size, color, and habitat, but can be distinguished by the hooked tip (retrolateral view) of the median apophysis in the male palpus and by the broad transverse median septum in the epigynum.

Range.—Alaska to Labrador, south to Arizona, New Mexico, and New Hampshire; Greenland; Europe and Asia.



Map 5.—Geographical distribution of *Arctosa alpigena* (Doleschall).



Figs. 33-45.—Structures of *Arctosa* spp.: 33-41, *A. alpigena* (Doleschall); 33, 34, epigyna; 35, 38, palpi of male, 35, ventral view, 38, retrolateral view; 36, 39, spermathecae; 37, compound seta; 40, body of female, dorsal view; 41, simple seta; 42-45, *A. insignita* (Thorell); 42, epigynum; 43, 44, palpi of male, 43, ventral view, 44, retrolateral view; 45, spermathecae.

Natural history.—Specimens of *A. apligena* have been collected in sphagnum bogs, lichen- or heath-covered ground in arctic and alpine tundra, in lodgepole pine forests, and in alpine meadows. Adults have been collected from early June to September 10.

Arctosa insignita (Thorell)

Figs. 42-45; Map 6

Trochosa insignita Thorell, 1872:160.

Arctosa insignita: Braendegaard 1939:5, figs. 1, 3; Bonnet 1955:649 (in part); Holm 1967:71, figs. 88, 89.

Tricca insignita: Lugetti and Tongiorgi 1966:147, fig. V (1-4).

Type data.—Female holotype from Disko, Greenland (C. Nystrom), in ZIU, examined.

Male.—Total length 5.3-8.3 mm. Carapace 3.55 ± 0.23 mm long and 2.69 ± 0.16 mm wide (20 specimens). Carapace dark red brown, with pale median area gradually widening anterior to dorsal groove, with few pale setae. Anterior row of eyes slightly procurved, nearly as long as middle row, with eyes approximately equal in size. Chelicerae red



Map 6.—Geographical distribution of *Arctosa insignita* (Thorell).

brown, darker distally; promargin of fang furrow with three teeth. Sternum dusky red brown, sometimes with pale median spot in anterior half. Legs red brown, with dark rings on femora and tibiae, with sparse copulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, two prolaterals, two retrolaterals; basitarsus I with two or three prolateral macrosetae (exclusive of any at tip), 0-3 retrolaterals (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen red brown, with dark brown or black reticulations; heart mark white densely covered with compound setae (Fig. 37); venter pale red brown or pale gray. Terminal apophysis of palpus with soft distal part and hard, slender basal part (Fig. 43); embolus long, slender, sinuous; median apophysis broad, drawn out to fine, straight tip (Figs. 43, 44).

Female.—Total length 6.9-10.9 mm. Carapace 3.69 ± 0.30 mm long and 2.81 ± 0.22 mm wide (20 specimens). General structure and color essentially as in male but tibia I without a dorsal macroseta. Epigynum with median septum approximately triangular in out line (Fig. 42). Copulatory tubes coiled; spermathecae bulbous (Fig. 45).

Diagnosis.—Specimens of *A. insignita* most resemble those of *A. alpigena*, being similar in size, color, and habitat, but are distinguished by the straight tip (retrolateral view) on the median apophysis of the male palpus and by the triangular median septum in the epigynum.

Range.—Alaska to Baffin Island, south to Colorado; Greenland.

Natural history.—*A. insignita* is mainly a spider of the open tundra. Many specimens have been collected by pitfall traps in Greenland and in the Canadian arctic; a few are known from alpine tundra in the Rocky Mountains. Adults have been collected from June 8 to the end of August.

Arctosa perita (Latreille)

Figs. 46-49; Map 7

Aranea perita Latreille, 1799:170.

Lycosa perita: Latreille, 1817:297; Simon 1937:1115, 1135, figs. 1754, 1755.

Lycosa picta Hahn, 1831:106, fig. 79.

Arctosa lynx C. L. Koch, 1848:133, fig. 1364.

Lycosa filicata Simon, 1876:277.

Arctosa perita: C. L. Koch 1848:133, figs. 1362, 1363; Dahl 1908:210; Dahl and Dahl 1927:69, 70, figs. 179, 180; Palmgren 1939:74, figs. 120, 121; Holm 1947:20, 21, fig. 6a, Pl. 4, figs. 40, 41, Pl. 9, fig. 20; Locket and Millidge 1951:284, figs. 137B, 138B; Wiebes 1959:32, figs. 38, 47, 53, 54; Roewer 1955:226; Bonnet 1955:656.

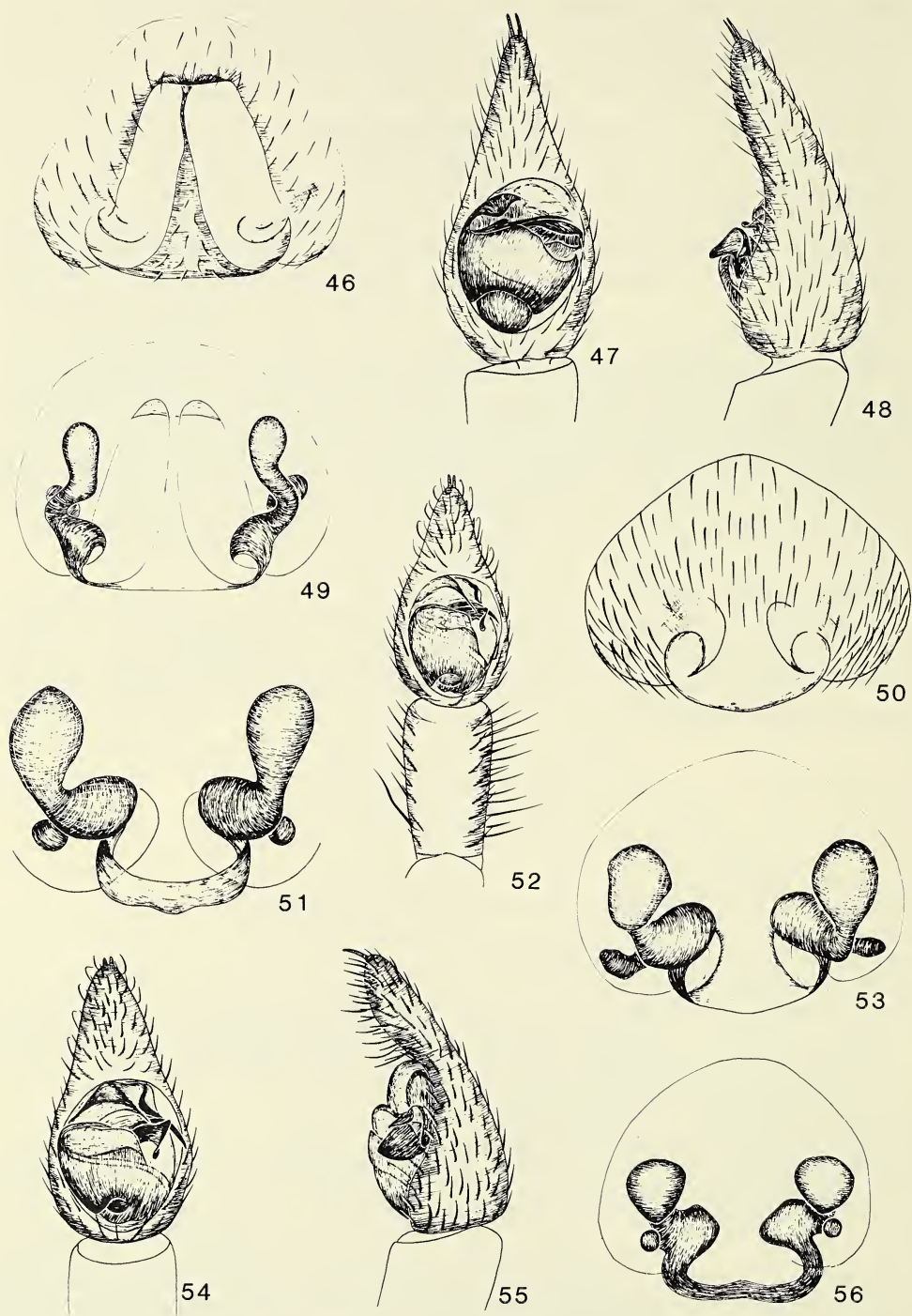
Arctosa perita arenicola Simon, 1937:1116, 1138.

Arctosella perita: Roewer 1960:672, figs. 381a, b.

Arctosa perita perita: Lugetti and Tongiorgi 1965:175, Pl. 2, figs. 1-4, Pl. 4, fig. 1; Fuhrn and Niculescu-Burlacu 1971:185, figs. 91 a-d.

Arctosa perita latithorax Lugetti and Tongiorgi, 1965:180, Pl. 4, fig. 2, Pl. 5, figs. 1-4.

Type data.—Type(s) of *perita* from France, no longer in existence (Roewer 1960:673); species identified from original description and from subsequent published descriptions. Male and female syntypes of *picta* from Nürnberg, Germany, not located. Three female syntypes of *lynx* from Nürnberg, Germany, not located. Type(s) of *filicata* from France, not located. Type(s) of *arenicola* from Gironde and Landes, France, not located. Female holotype, two male paratypes, and one female paratype of *latithorax* from S. Rossore, Pisa, Italy, May 3 1963 (Tongiorgi), in Museo di Storia Naturale di Genova, not examined.



Figs. 46-56.—Genitalia of *Arctosa* spp.: 46-49, *A. perita* (Latreille); 46, epigynum; 47, 48, palpi of male, 47, ventral view, 48, retrolateral view; 49, spermathecae; 50-56, *A. minuta* F. Pickard-Cambridge; 50, epigynum; 51, 53, 56, spermathecae; 52, 54, 55, palpi of male, 52, 54, ventral view, 55, retrolateral view.

Male.—Total length 5.3-6.3 mm. Carapace 3.01 - 3.40 mm long and 2.15 - 2.59 mm wide (five specimens). Carapace brown or dark brown, with black radiating lines, and with irregular pale median area and pale submarginal spots, sparsely covered with pale setae. Anterior row of eyes straight or slightly procurved, nearly as long as middle row, with median eyes slightly larger than lateral eyes. Chelicerae dark brown; promargin of fang furrow with two or three teeth. Sternum dark brown to black. Legs pale yellow brown, with dark rings on femora, tibiae, and basitarsi, with sparse scopulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, two prolaterals, no retrolaterals; basitarsus I with one or two prolateral macrosetae (exclusive of any at tip), no retrolaterals (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen dark brown to black, mottled with yellow brown; heart mark pale brown or yellow brown; venter pale brown, sometimes with broad dusky longitudinal band. Terminal apophysis of palpus with basal area sclerotized (Fig. 47); embolus long, nearly straight; median apophysis elongate, not tapered, with deep channel along distal surface (Figs. 47, 48).

Female.—Total length 7.4 - 7.5 mm. Carapace 3.06, 3.31 mm long and 2.22, 2.48 mm wide (two specimens). General structure and color essentially as in male. Epigynum with median septum slender anteriorly and gradually widening posteriad (Fig. 46). Copulatory tubes thick, curved; spermathecae bulbous (Fig. 49).

Diagnosis.—*A. perita* is unique among the American species of *Arctosa* in having a combination of dark sternum, no retrolateral macrosetae on tibia and basitarsus I (exclusive of any at tip of basitarsus), simple setae covering the abdominal heart mark, the anterior median eyes only slightly larger than the anterior lateral eyes, and a gradually widened epigynal septum. The small size is also diagnostic value. *A. perita* appears to have been recently introduced into the American fauna.

Range.—Vancouver, British Columbia; Europe, Asia, North Africa.

Natural history.—In Europe, *A. perita* is found in sand dunes and sandy heaths, where the females make their silk-lined burrows. Wiebes (1959) gives the period of maturity as August to the following May, with mating in April and May. The British Columbia specimens were collected on open ground on Burnaby Mountain in late May.

Arctosa minuta F. Pickard-Cambridge

Figs. 50-56; Map 7

Arctosa minuta F. Pickard-Cambridge, 1902:331, Pl. 31, figs. 26, 27; Bonnet 1955:654; Roewer 1955:230.

Arctosa cheluncata Petrunkevitch, 1925:177, figs. 94-96; Bonnet 1955:643. NEW SYNONYM. *Arkalosula cheluncata*: Roewer 1955: 232.

Type data.—Male holotype and female allotype of *minuta* from Guatemala (Sarg), in BMNH, examined. One female syntype of *cheluncata* from Remedios, Panama, in PMNH, examined; two male, three female, and one juvenile syntype of *cheluncata* from Santiago, Panama, in PMNH, examined; one male, one female, and one juvenile syntype of *cheluncata* from Wilcox camp, San Lorenzo River, Panama, in PMNH, examined; one juvenile syntype of *cheluncata* from La Mesa, Panama, in PMNH, examined.

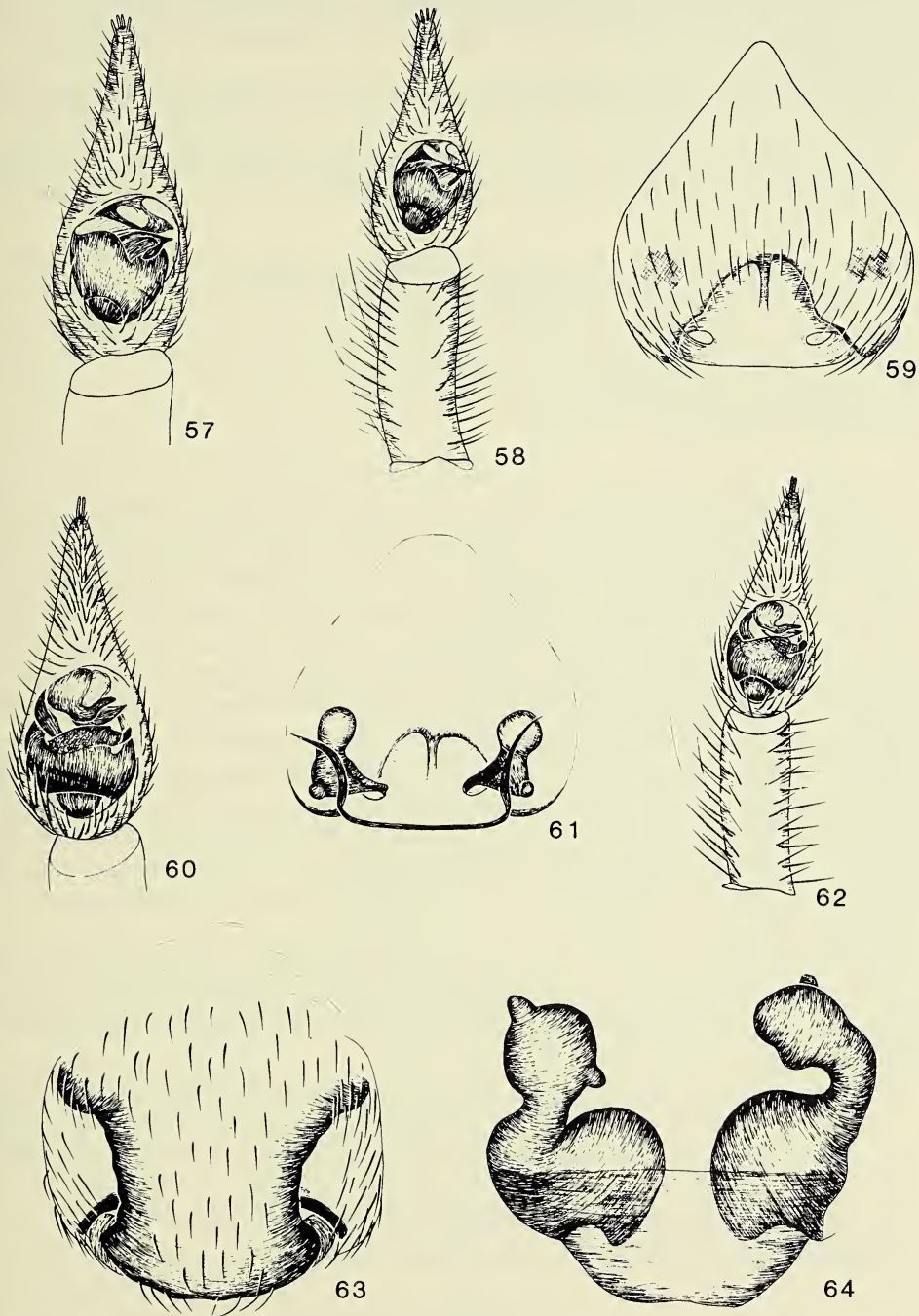
Male.—Total length 4.8 - 8.0 mm. Carapace 3.53 ± 0.40 mm long and 2.66 ± 0.29 mm wide (12 specimens). Carapace pale yellow, mottled with pale to dark brown, with few pale setae. Anterior row of eyes slightly procurved, nearly as long as middle row, with

median eyes larger than lateral eyes. Chelicerae pale to dark brown, often with large pale spot on basal half; promargin of fang furrow with two teeth; fang with prominence on outer surface. Sternum pale yellow. Legs yellow to yellow brown, with brown rings on most segments, with sparse scopulae; femur I with three dorsal macrosetae, one or two prolaterals near tip; tibia I with no dorsal macrosetae, two prolaterals, two retrolaterals; basitarsus I with three prolateral macrosetae (exclusive of any at tip), two or three retrolaterals (exclusive of any at tip); tibia III with two dorsal macrosetae. Abdomen pale yellow to yellow brown, mottled with dusky brown; heart mark and venter pale yellow. Terminal apophysis of palpus with broad distal part and thin, flat, curved basal part (Fig. 54); embolus short, curved; median apophysis with broad, thin process directed ventrad (Figs. 54, 55).

Female.—Total length 7.0 - 9.0 mm. Carapace 4.02 ± 0.36 mm long and 3.09 ± 0.28 mm wide (20 specimens). General structure and color essentially as in male, but anterior row of eyes sometimes straight and equal in length to middle row. Epigynum with short, broad median septum (Fig. 50). Copulatory tubes short, stout; spermathecae bulbous (Figs. 51, 53, 56).



Map 7.—Geographical distribution of *Arctosa* spp.: *A. perita* (Latreille), open star; *A. minuta* F. Pickard-Cambridge, circles; *A. sanctaerosae* Gertsch and Wallace, solid stars; *A. serii* Roth and Brown, triangles.



Figs. 57-64.—Genitalia of *Arctosa* spp.: 57-59, 61, *A. serii* Roth and Brown; 57, 58, palpi of male, ventral view; 59, epigynum; 61, spermathecae; 60, 62-64, *A. sanctaerosae* Gertsch and Wallace; 60, 62, palpi of male, ventral view; 63, epigynum; 64, spermathecae.

Diagnosis.—Specimens of *A. minuta* are distinguished from those of other species by the combination of two well developed dorsal macrosetae on tibia III, the broad, thin process on the median apophysis of the male palpus, and the short, broad median septum of the epigynum.

Range.—Southern Texas through Mexico and Central America to Colombia and Guyana.

Natural history.—The type-series was collected under stones in drying stream beds. Adults were collected from late March to the end of May.

Arctosa sanctaerosae Gertsch and Wallace

Figs. 60, 62-64; Map 7

Arctosa sanctae-rosae Gertsch and Wallace, 1935:5, figs. 23, 24.

Arctosa sanctaerosae: Bonnet 1955:661.

Arkalosula sanctae-rosae: Roewer 1960: 761.

Type data.—Male holotype, female allotype, and male and female paratypes from Santa Rosa Island, Pensacola, Florida, April 5 1934 (H. K. Wallace), in AMNH, examined.

Male.—Total length 8.2 - 13.2 mm. Carapace 5.69 ± 0.44 mm long and 4.12 ± 0.45 mm wide (19 specimens). Carapace pale orange to off-white, not mottled, with few pale setae. Anterior row of eyes straight or slightly recurved, distinctly shorter than middle row, with median eyes twice as large as lateral eyes. Chelicerae pale orange or off-white; promargin of fang furrow with three teeth. Sternum pale orange or off-white. Legs pale orange or off-white, without dark rings, with rather dense scopulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with one dorsal macroseta, two prolaterals, two retrolaterals; basitarsus I with three prolateral macrosetae (exclusive of any at tip), three retrolaterals (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle. Abdomen chalk white, with pale orange heart mark; venter white. Terminal apophysis of palpus with large, soft distal part and slender, curved basal part (Fig. 60); embolus long, curved; median apophysis long, with curved tip, and with groove along distodorsal surface.

Female.—Total length 10.9 - 12.0 mm. Carapace 5.44 ± 0.52 mm long and 3.89 ± 0.37 mm wide (19 specimens). General structure and color essentially as in male. Epigynum with large, convex median septum (Fig. 63). Copulatory tubes thick; spermathecae bulbous (Fig. 64).

Diagnosis.—Specimens of *A. sanctaerosae* are distinguished from those of other species of *Arctosa* by the pale orange (or white) body and legs, by the presence of a dorsal macroseta on tibia I, and by the broad, convex median septum and stout copulatory tubes.

Range.—Gulf of Mexico coast from Mississippi to the Florida panhandle.

Natural history.—*A. sanctaerosae* lives on sandy beaches.

Arctosa littoralis (Hentz)

Figs. 65-74; Map 8

Lycosa littoralis Hentz, 1844:388, Pl. 17, fig. 9.

Lycosa maritima Hentz, 1844:389, Pl. 17, fig. 10.

Lycosa cinerea: Emerton 1885:488, Pl. 47, figs. 3, 3a, 3b; 1902:73, figs. 177, 178; Montgomery 1902:555, Pl. 29, figs. 17, 18; Chamberlin 1908:281, Pl. 20, fig. 6.

Trochosa cinerea: Stone 1890:428; Montgomery 1904:305, Pl. 20, fig. 43.

Arctosa trifida: F. Pickard-Cambridge, 1902:330, Pl. 31, figs. 24, 25; Gertsch and Wallace 1935:5; Bonnet 1955:661; Roewer 1955:231. NEW SYNONYM.

Arctosa panamana Petrunkevitch, 1925:179, fig. 97; Banks 1929:83; Bonnet 1955:655. NEW SYNONYM.

Arctosa littoralis: Gertsch 1934:7; 1935:19; Gertsch and Davis 1940:6; Kaston 1948:320, Pl. 53, fig. 1050, Pl. 55, figs. 1070, 1071; 1978:189, fig. 481; Levi and Field 1954:455; Bonnet 1955:653; Roth and Brown 1976:61, figs. 3, 6, 8.

Arctosa cinerea: Roewer 1955:227 (in part).

Arkalosula panamana: Roewer 1955:232.

Type data.—Type(s) of *littoralis* from North Carolina, April, no longer in existence; species identified from original description and illustration. Type(s) of *maritima* from Bear Island, St. Helena Bay, South Carolina and from Salem, Massachusetts, no longer in existence. Male holotype of *trifida* from Teapa, Mexico (H. S.), not located; two female paratypes of *trifida* from Teapa, Mexico, in MBNH, examined; paratypes of *trifida* from Santa Ana and Guatemala City, Guatemala, not located. Female holotype of *panamana* from Remedios, Panama, February 27 1924 (A. and W. Petrunkevitch), in PMNH, examined.

Male.—Total length 9.6 - 12.8 mm. Carapace 6.06 ± 0.63 mm long and 4.69 ± 0.49 mm wide (20 specimens). Carapace pale, with lateral areas mottled and marked with pale longitudinal band and with pale spot near each leg base (as in fig. 66), with few pale setae. Anterior row of eyes straight or slightly procurved, slightly shorter than middle row, with median eyes about twice as large as lateral eyes (Fig. 65). Chelicerae dark red brown; promargin of fang furrow with two teeth; fang with prominence on outer surface. Sternum pale yellow or pale brown. Legs yellow brown, darker distally, usually with faint brown rings, and with sparse scopulae; femur I with three dorsal macrosetae, two prolaterals near tip; tibia I with no dorsal macrosetae, two prolaterals, two retrolaterals; basitarsus I with three prolateral macrosetae (exclusive of any at tip), two or three retrolaterals (exclusive of any at tip); tibia III with one dorsal macroseta plus a basal bristle, and with three retrolaterals. Abdomen yellow to yellow brown, with light brown heart mark and with brown reticulations; venter pale yellow. Terminal apophysis of palpus with long, narrow sclerotized part lying parallel with embolus; embolus long, straight, deeply grooved; median apophysis long, stout, strongly angled basad near tip (Figs. 69, 73).

Female.—Total length 11.2 - 14.7 mm. Carapace 6.08 ± 0.51 mm long and 4.88 ± 0.42 mm wide (20 specimens). General structure and color essentially as in male but chelicerae lacking outer prominence, and leg scopulae more dense (particularly on leg I). Epigynum variable, with median septum usually broad, concave at sides (Figs. 67, 68, 70, 71). Copulatory tubes short, thick; spermathecae bulbous (Figs. 72, 74).

Diagnosis.—Specimens of *A. littoralis* resemble those of *A. minuta*, *A. sanctaerosae*, and *A. serii* in having the anterior median eyes distinctly larger than the anterior lateral eyes. They differ from those of *minuta* by possessing only one dorsal macroseta (plus a basal bristle) on tibia III, from those of *sanctaerosae* by having only two teeth on the promargin of the cheliceran fang furrow, and from those of *serii* by having two prolateral macrosetae near the tip of femur I, three retrolateral macrosetae on tibia III, and (usually) dark rings on the legs. Males of *littoralis* further differ from those of the other species mentioned by the long narrow terminal apophysis on the palpus, and females further differ by the broad, laterally-concave median septum of the epigynum.

Range.—Interior British Columbia to Nova Scotia, south to Panama.

Natural history.—Specimens of *A. littoralis* are found, at night, running on beaches; Stone (1890) observed them in the wake of retreating breakers in New Jersey. They

ensconce themselves under driftwood during daylight hours. Kaston (1948) observed the burrows, which are 15-25 cm deep. Adults have been collected from February to November.

Arctosa serii Roth and Brown

Figs. 57-59, 61; Map 7

Arctosa littoralis: Chamberlin 1924:673 (in part).

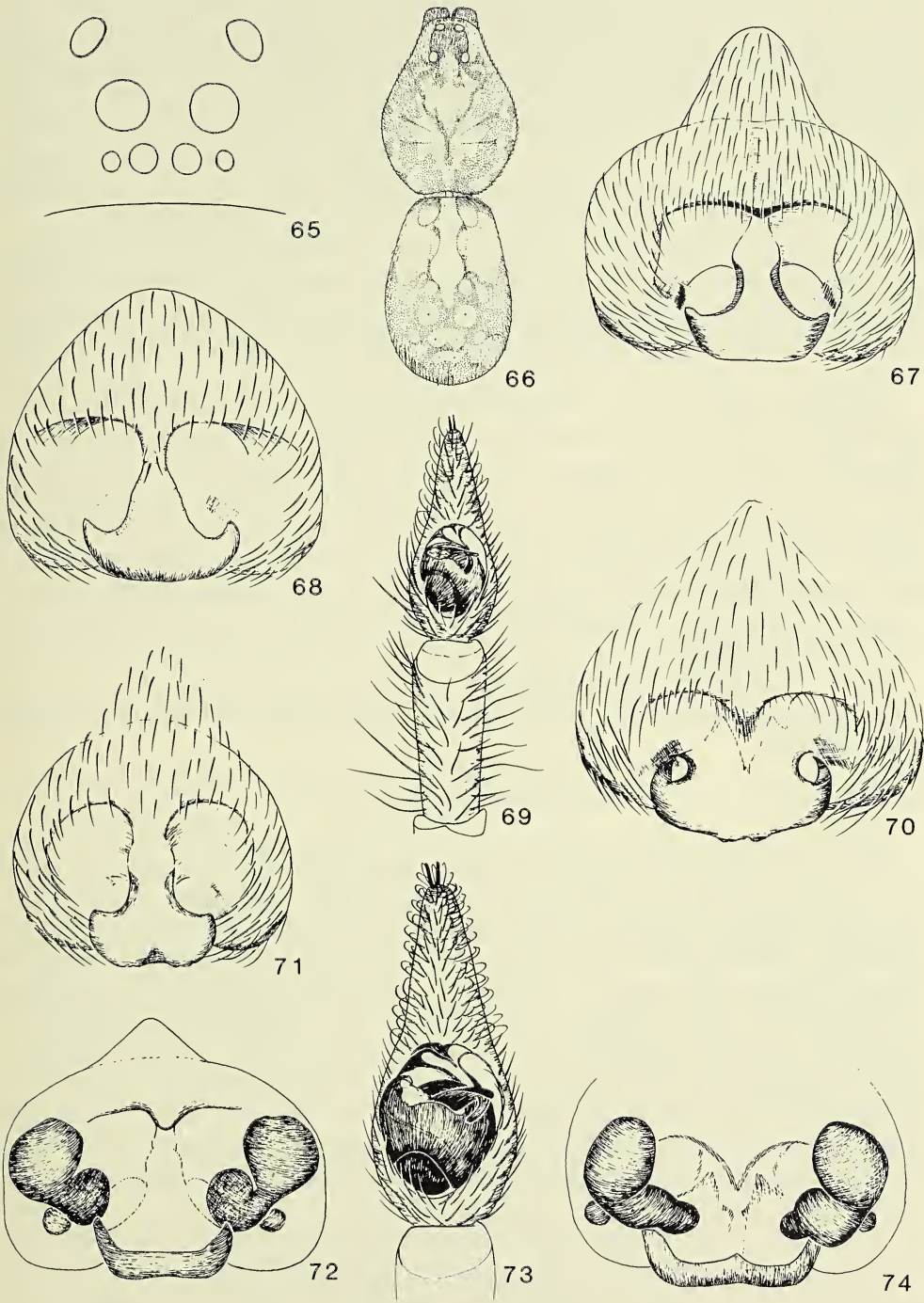
Arctosa serii Roth and Brown, 1976:61, figs. 1, 2, 4, 5, 7.

Type data.—Male holotype, female allotype, and male and female paratypes from El Desemboque, Sonora, Mexico, March 4 1974 (H. Flanders), in AMNH, examined; paratypes from San Pedro Bay, Sonora, in AMNH, examined.

Male.—Total length 11.0 - 12.0 mm. Carapace 6.46 ± 0.39 mm long and 4.79 ± 0.35 mm wide (11 specimens). Carapace pale yellow to orange, with few darker radiating lines, sometimes with faint brown mottling on lateral areas, with few pale setae. Anterior row of eyes straight or slightly procurved, somewhat shorter than middle row, with median eyes about twice as large as lateral eyes. Chelicerae dark red brown; promargin of fang



Map 8.—Geographical distribution of *Arctosa littoralis* (Hentz).



Figs. 65-74.—Structures of *Arctosa littoralis* (Hentz): 65, eyes, frontal view; 66, body of female, dorsal view; 67, 68, 70, 71, epigyna; 69, 73, palpi of male, ventral view; 72, 74, spermathecae.

furrow with two teeth; fang with prominence on outer surface. Sternum pale yellow to yellow brown. Legs straw yellow, without dark rings, with sparse scopulae; femur I with three dorsal macrosetae, one prolateral near tip; tibia I with no dorsal macrosetae, two prolaterals, two retrolaterals; basitarsus I with three prolateral macrosetae (exclusive of any at tip), three retrolaterals (exclusive of any at tip); tibia III with one dorsal macroseta (lacking basal bristle), two retrolaterals. Abdomen pale to bright yellow, with pale brown heart mark and a few brown or dusky lateral marks; venter pale yellow. Terminal apophysis of palpus broad, bladelike, tapered abruptly at tip (Fig. 57); embolus long, broad, grooved; median apophysis long, stout, strongly angled near tip (Fig. 57).

Female.—Total length 12.0 - 14.4 mm. Carapace 6.39 ± 0.53 mm long and 4.79 ± 0.42 mm wide (20 specimens). General structure and color essentially as in male, but cheliceral fang lacking prominence on outer surface. Epigynum with incomplete median septum (Fig. 59). Copulatory tubes broad, swollen on lateral side; spermathecae bulbous (Fig. 61).

Diagnosis.—Specimens of *A. serii* resemble those of *A. minuta*, *A. sanctaerosae*, and *A. littoralis* in having the anterior median eyes distinctly larger than the anterior lateral eyes. They differ from those of *minuta* in having only one dorsal macroseta on tibia III, from those of *sanctaerosae* by having only two teeth on the promargin of the cheliceral fang furrow, and from those of *littoralis* in having only one prolateral macroseta on femur I, only two retrolateral macrosetae on tibia III, and no dark rings on the legs. Males of *serii* further differ from those of the other species by the broad, bladelike, abruptly - tapered terminal apophysis on the palpus, and females further differ by the incomplete median septum of the epigynum.

Range.—Shores of the Gulf of California.

Natural history.—Roth and Brown (1976) state that *A. serii* is found only at the drift line of beaches.

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SPATIAL AND TEMPORAL PATTERNS IN A SAGEBRUSH STEPPE SPIDER COMMUNITY (ARACHNIDA, ARANEAE)

Barbara J. Abraham ¹

Department of Biology and Ecology Center
Utah State University
Logan, Utah 84322

ABSTRACT

A total of 83 species of spiders were collected from the shrub, herb and ground strata of a sagebrush steppe in northern Utah. Dominant families (Thomisidae, Philodromidae, Salticidae) and, in some cases, genera (*Misumenops*, *Philodromus*) or species [*Sassacus papenhoei* (Peckham and Peckham)] were similar to those found in other studies of shrub-dominated areas. Among the spiders of this community, ambushing and wandering were more common foraging strategies than was webspinning.

Habitat separation in sagebrush steppe spiders was more vertical than horizontal. Shrub and herb spider species assemblage differed sharply from the ground spider species assemblage, less so from one another. Differences in vegetation density, diversity and size among four study plots correlated positively with spider abundance and diversity, but resulted in less difference among spider assemblages.

Temporal patterns of spider abundance differed among strata. Seasonal patterns showed evidence of being influenced by climate and migration of spiders between strata. Diel activity patterns were examined only for spiders of shrub and herb strata. Spider activity in the herb stratum was strongly influenced by light intensity, temperature and relative humidity. This was not as clear in shrubs.

INTRODUCTION

In order to understand the structure and processes of spider communities in shrub-dominated areas, one must obtain knowledge of the distributions of spiders in shrub, herb and ground strata. With the exception of Gertsch and Riechert (1976), few studies have accomplished this. Most studies have examined the spiders of one community stratum. For example, Chew (1961) and Chaplin (1976) studied the spiders of hot and cold desert shrubs, respectively. Fautin (1946) included data on shrub stratum spiders in his study of western Utah biotic communities, and Hatley and MacMahon (1980) outlined seasonal distributions of spiders in sagebrush. Turner (1962) included ground stratum spiders in his sampling study of plants and arthropods in Arizona desert.

Other spider studies in shrub-dominated areas have concentrated on single species (e.g., Riechert 1974) or families (e.g., Bixler 1970). Habitat partitioning among some common sagebrush steppe spiders was examined by Robinson (1981).

¹ Present address: Department of Biological Sciences, Hampton Institute, Hampton, VA 23668

The purposes of the present study are: (1) To describe the taxonomic composition of the spider community of a sagebrush steppe in northern Utah; (2) To describe and compare distributions of spider species, families and foraging strategies (ambushing, wandering, webspinning) (a) among shrub, herb and ground strata, (b) among study plots having a continuum of vegetation types (herbaceous—herbaceous/shrubby—shrubby), (c) seasonally and (d) through the day; (3) To examine correlations of spider distributions with climatic variables and characteristics of the vegetation (density, diversity, cover, height, volume).

STUDY AREA

The study was conducted on the upper alluvial fan at the mouth of Green Canyon, Cache Co., Utah (elevation 1512 m). Mean annual temperature for the area is 7.9°C; mean annual precipitation is 46.8 cm (mostly snow); mean number of frost-free days is 145 (A. Richardson, Utah State Climatologist, personal communication).

Vegetation is sagebrush steppe, dominated by *Artemisia tridentata* (Pursh) Scribn. and Smith. Other shrubs in the area are *Amelanchier alnifolia* Nutt., *Chrysothamnus nauseosus* (Pall.) Britton, *Gutierrezia sarothrae* (Pursh) Britton and Rusby, and *Rosa woodsii* Lindl. Grasses are *Agropyron spicatum* (Pursh) Scribn. and Smith, *Bromus brizaeformis* Fischer and Meyer, *B. commutatus* Schrader, *B. tectorum* L., *Poa bulbosa* L., *P. pratensis* L., *Secale cereal* L., and *Stipa* sp. Some abundant herbaceous species are *Alyssum alyssoides* L., *Erodium cicutarium* L'Her., and *Ranunculus testiculatus* Crantz., which are very small and carpet the ground in some areas. Other common herbs on the study site are *Achillea millefolium* L., *Artemisia ludoviciana* Nutt., *Astragalus cibarius* Sheld., *Balsamorhiza sagittata* (Pursh) Nutt., *Camelina microcarpa* Andr., *Crepis occidentalis* Nutt., *Cymopterus longipes* S. Wats., *Hackelia patens* (Nutt.), *Lithospermum ruderae* Dougl., *Phacelia linearis* (Pursh), *Solidago canadensis* L., *Sonchus oleraceus* L., *Tragopogon dubius* Scop., and *Wyethia amplexicaulus* Nutt.

Soil at the canyon's mouth (on which were Study Plots, 2, 3 and 4) was Loamy-skeletal, mixed, mesic Typic Calcixeroll. On the slope above the alluvial fan (containing Plot 1) soil was Loamy-skeletal, carbonatic, mesic Typic Haploxeroll (Erickson and Mortensen 1974). Stones were numerous on the surface of Plot 1.

METHODS

Study Plots.—Four 3600 m² study plots were established and subdivided into 12 x 12 m squares. Vegetation was sampled on the plots in June and July 1974. Density, height, cover and volume (formulae as in Hatley and MacMahon 1980) of shrubs were determined in 10 randomly located 2 m x 8 m quadrats within each plot. Density, cover class (Daubenmire 1959) and height class (0-25 cm, 26-50 cm, 51-75 cm, over 75 cm) were determined for each herb species in seven 20 cm x 50 cm microplots within each 2 m x 8 m quadrat.

Spider Sampling.—Spiders were sampled from August through September 1974, June through October 1975 and May through November 1976. Three of the four study plots burned in a range fire in July 1976; subsequent sampling was completed in the remaining plot (#1). As a consequence, number of samples in the plots differed.

Spiders in herbaceous vegetation were sampled with a sweep net, by taking 100 sweeps while walking 100 paces parallel to plot grid stakes. Four 100-sweep samples were taken at each sampling time. Subsequent samples in the same area were taken at intervals of at least two weeks. The total number of 100-sweep samples was 458.

Shrub-inhabiting spiders were dislodged by beating shrubs with a stick, knocking the spiders onto sheets. Three shrubs were sampled at each sampling time. Except in Plot 1, no shrub was sampled more than once. A total of 354 shrubs were sampled.

Ground-dwelling spiders were sampled with pitfall traps similar to those of Uetz and Unzicker (1976), but without a rim. A sampling station consisted of three pitfall traps located within 30 cm of each plot grid stake. Each plot had 108-111 pitfalls. Pitfall samples in the same area were taken at intervals of at least two weeks. Samples varied in number of trap-hours; total trap-hours were 22,329.

Discussion of these sampling methods may be found in Uetz and Unzicker (1976) and Southwood (1978). Turnbull (1973) concluded that the sampling method of choice depends upon the community to be sampled. I chose the above methods because: (1) No absolute densities were to be calculated; (2) Samples were to be taken by one person, frequently at night; and (3) These methods are inexpensive, easy to use, and relatively immune to equipment failure. Realizing that no completely error-free method for quantitative sampling of small, active arthropods exists, I am satisfied that my methods adequately surveyed the spider fauna. Graphs of cumulative sample variance of spider families against randomized accumulated samples in each stratum indicated adequate sampling after 50 samples (Figure 1). Similar curves for species did not quite level off after 300 samples for shrub and ground strata, perhaps due to rare immigrants from adjacent communities.

All spiders were picked from samples in the field and preserved for laboratory identification. Species, sex (if determinable) and body length excluding spinnerets were recorded for each specimen. Species were kindly identified by Dr. W. J. Gertsch.

Local Environment—Time of day, temperature, relative humidity and light intensity were recorded before and after each sampling period. During 1975 and 1976 a hygrothermograph and an actinograph also recorded continuous data on the study site. Monthly precipitation data were obtained from a weather station in North Logan (one km from the study site) (Figure 2).

Spider Data Analysis.—Data on shrub-, herb- and ground-dwelling spiders were analyzed separately because of the different sampling techniques used in each stratum. For seasonal patterns, the data were grouped into 15 biweekly intervals beginning 5 May (first sample) and ending 29 November (last sample). For daily patterns, data were numbered

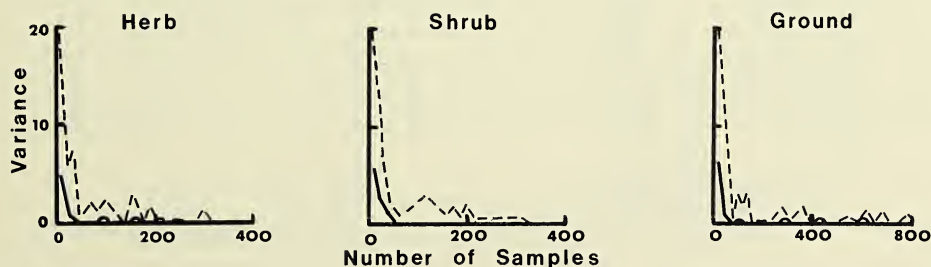


Fig. 1.—Variance in number of spider families (solid lines) and species (broken lines) in randomized, accumulated samples from community strata at Green Canyon, Cache Co., Utah.

by midpoint of sampling time (e.g., 0730–0829 = 0800 hr). Data on ground-inhabiting spiders could not be analyzed hourly, because sampling duration was greater than one hour. (Few ground spiders were captured in one hour.)

Spider diversities were calculated using the Shannon-Wiener Diversity Index (Shannon and Weaver 1949). Horn's (1966) Index of Overlap was chosen to examine similarity of spider assemblages in space and time. Any two spider assemblages scoring over 85% on Horn's Index were considered arbitrarily "similar". Huhta (1979) listed Horn's Index as one of six indices which gave consistent results; Linton, Davies and Wrona (1981) found that Horn's Index was as accurate as other overlap indices between 75 and 100% overlap.

For some analyses, spider families were grouped into three foraging strategies (ambushing, wandering, webspinning; see Appendix). These categories were largely based on accounts in the literature (e.g., Gertsch 1979) and personal observation of spider hunting. This method assumes a constant foraging strategy within spider families. Spider families are constructed on the basis of morphology, which is often correlated with the method of prey capture. Post and Riechert (1977) thought that adaptive syndromes such as hunting techniques emerge at the family level rather than at the species level in spiders.

An initial five-way analysis of variance (ANOVA) was used to determine whether interactions between variables were significant. The five variables were stratum, plot, year, biweekly interval and time of day. Interactions were not significant, and years were not significantly different. Spider data for the three study years were therefore lumped, and compared in spatial (plots) and temporal (biweekly, hourly) categories within strata by one-way ANOVA. Student-Newman-Keuls Multiple Range Tests (SNKMRT) for unequal sample sizes were performed on means when ANOVA was significant. (In this paper, statistical significance is $P = 0.05$ or less unless otherwise noted.) Since SNKMRT is not as powerful a test as ANOVA, it did not always detect which means were different.

Abundance of individuals and dominant spider families was regressed against characteristics of the vegetation. Since sampling the vegetation of the four study plots gave only four data points, two-variable linear regressions were employed to compare one vegetation parameter at a time with spider abundance.

Spider abundances were used in stepwise multiple regressions against the following components of local environment: temperature, relative humidity, light intensity, vapor

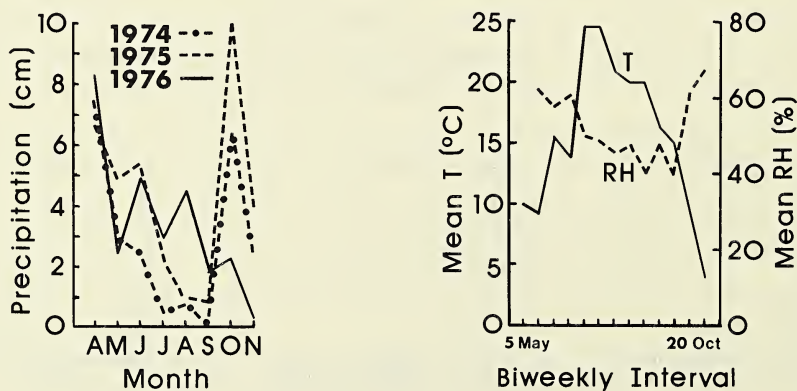


Fig. 2.—Seasonal weather patterns at Green Canyon, Cache Co., Utah. Monthly precipitation curves are from the North Logan weather station; temperature and relative humidity curves are from a hygrothermograph on the study site (1975 only).

pressure deficit and hours of daylight on the sampling date. Biweekly averages of temperature, relative humidity, minimum temperature and daily high light intensity during 1975 were used to test for longer-term relationships.

RESULTS AND DISCUSSION

Taxonomic Composition and Vertical Stratification of the Spider Community.—

In the present study, 11,098 spiders representing 83 species and 18 families (see Appendix) were collected from a combined area of slightly over one ha (10,800 m²). Table 1 summarizes spider sampling data from shrub, herb and ground strata. When all vertical strata of a community are examined, more spider species appear than are present in one stratum alone. Hatley and MacMahon (1980), working only in the shrub stratum at Green Canyon, found 40 species of spiders, as compared to 83 species found in all community strata by the present study. Turner (1962) found that ground stratum spiders of the Arizona desert were completely different (with the exception of one *Oxyopes* specimen) from those swept from Arizona desert shrubs by Chew (1961).

Table 2 summarizes the numerically dominant spider families and species in each community stratum. Thomisidae was by far the dominant in herbs, while Lycosidae, Gnaphosidae and Thomisidae were numerically dominant on the ground. In shrubs, dominant families were Salticidae, Theridiidae, Philodromidae and Thomisidae. Only two spider species in herbs [*Misumenops lepidus* (Thorell) and *Xysticus cunctator* Thorell], three in shrubs [*Theridion neomexicanum* Banks, *Sassacus papenhoei* (Peckham and Peckham) and *Philodromus histrio* (Latreille)] and three on the ground (*Schizocosa wasatchensis* Chamberlin and Ivie, *Xysticus montanensis* Keyserling and *Drassyllus nannellus* Chamberlin and Gertsch) attained 10% of the spider fauna of their respective stratum.

Comparing these results to those of other studies in shrub-dominated areas shows some similarities. Fautin (1946) recorded spiders of Utah cold desert shrubs; Chew (1961) studied spiders in Arizona creosotebush (*Larrea*); Chaplin (1976) worked with spiders of Nevada greasewood (*Sarcobatus*) and shadscale (*Atriplex*). *S. papenhoei*, a jumping spider, was a dominant in shrubs of Chew's, Chaplin's and the present study, and in one of Fautin's areas. *Philodromus*, a philodromid crab spider, was important in all four studies, and *Misumenops*, a crab spider, was dominant in Chew's, Fautin's and the present study.

Comparison of these four studies also revealed differences. In all studies but Chew's, one dominant species was a web spider. In Chaplin's study, *Dictyna*, a cribellate cobweb weaver, was numerically dominant during mid- and late summer. *Meteteira foxi* Gertsch and Ivie, an orb weaver, was common in Fautin's study. Both of these species were common in the present study, but *T. neomexicanum*, a combfooted cobweb weaver, was the most abundant spider in shrubs. Chew attributed a relative lack of web spiders in hot desert shrubs to flexible shrubs, wind, and less well-developed vegetational stratification in hot deserts.

The Green Canyon study site had strong morning and evening "canyon winds", but sagebrush steppe has a better-developed herbaceous stratum than hot desert, and cold desert shrubs such as greasewood, shadscale and sagebrush supply less flexible, less open substrate than does creosotebush. Robinson (1981) reported that *T. neomexicanum* and *M. lepidus* were the most abundant spiders collected from experimental habitat modules placed near the Green Canyon plots used in the present study. He found that *M. lepidus*

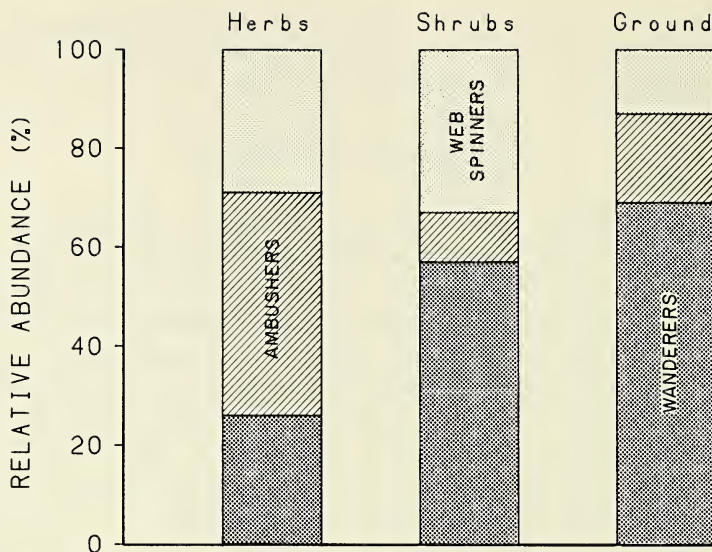


Fig. 3.—Relative abundance of three spider foraging strategies among individuals in herb, shrub and ground strata of the sagebrush steppe at Green Canyon, Cache Co., Utah.

showed no preference for open or closed, horizontal or vertical substrate, whereas *T. neomexicanum* preferred closed habitat. Hatley and MacMahon (1980), also working at Green Canyon, found that web spiders (mostly *Theridion* spp.) on sagebrush preferred dense to open foliage. They found no preference for dense or open foliage in running spiders (mostly *P. histrio*). These results combine to clarify the dominance of crab spiders (*Misumenops* and *Philodromus*) in both the hot desert and cold desert shrubs which have been studied: they are habitat generalists. Conversely, web spiders such as *Theridion* and *Dictyna* are probably limited in their distributions by shrub architecture.

At the species level, web spiders can be important members of shrub-dominated communities. However, capturing prey in webs is less common than other foraging strategies used by spiders in these areas. One spider foraging strategy reached its peak abundance in each stratum of the sagebrush steppe (ambushers in herbs, wanderers on the ground and webspinners in shrubs) (Figure 3). In herbs and on the ground, these respective strategies were dominant, but even in shrubs wanderers were more abundant than webspinners. Chew (1961) found that 94% of individuals and 79% of species in shrubs were non-webspinners (crab spiders and jumping spiders). Chaplin (1976) found shrub spider biomass to be dominated by crab spiders and jumping spiders. Fautin (1946) found 70% of shrub spider species to be non-webspinners. In the sagebrush of the present study, non-webspinning spiders comprised 67% of individuals and 55% of species sampled. Herb and ground stratum spiders were dominated by non-webspinners to an even greater degree.

Chew's (1961) finding that the spider community of hot desert shrubs is dominated by non-webspinning spiders can be generalized to include all strata of shrub-dominated areas. In spite of differences in rainfall, shrub architecture and vertical stratification among hot and cold deserts and sagebrush steppe, there remains a "shrub community spider fauna" characterized by dominance of non-webspinning spiders.

Post and Riechert (1976) found that dominant spiders were often habitat generalists. Most spider taxa collected from vegetation in the present study were found in both herb

Table 1.—Characteristics of the spider community in vertical strata of the sagebrush steppe at Green Canyon, Cache Co., Utah.

Characteristic	Herbs	Stratum Shrubs	Ground
No. of spiders collected	6633	2874	1591
No. of spider families	14	13	16
No. of spider species	61	55	50
diversity (H')	2.652	2.659	2.632
evenness (J')	0.645	0.664	0.673

and shrub strata. The top dominant species in herbs and shrubs (Table 2) were each over 5% of the spider fauna in the other vegetative stratum. (Each stratum had only 3-6 species which were over 5% of the spider fauna. See Appendix.) Pairwise comparisons of Green Canyon spider assemblages in strata showed much more similarity between the vegetational strata than between either vegetational stratum and the ground (Table 3). The herb stratum seemed to function as an ecotone, separating typical ground and shrub spider communities, with additional species begin most common in this "edge" habitat. This resulted in both the highest species richness and the highest dominance being observed in herb stratum spiders (Table 1).

Turnbull (1960) found that the field layer (herb stratum) in English oak woods contained spiders from both ground and canopy strata. Luczak (1966, in Turnbull 1973) attributed the greatest number of spider species and individuals to the field layer. She suggested that this might cause competition, forcing spiders to migrate upward. Lowrie (1968) documented movement of mature wandering spiders out of the herb stratum, into both ground and canopy layers.

In the present study the ground spider fauna was most restricted; no ground dominant was taken regularly in vegetation. [Robinson (1981) identified a dominant on his artificial habitat modules at Green Canyon as *X. montanensis*, a species which was restricted to

Table 2.—Numerically dominant spider species and families from vertical strata of the sagebrush steppe at Green Canyon, Cache Co., Utah. Prominence of Thomisidae in shrubs is due to cumulative abundance of several species each comprising less than 10% of shrub spiders. For number captured and relative abundance of each species, see Appendix.

DOMINANTS				
Stratum	Family Rank	Family	Species	Species Rank
Herbs	1	Thomisidae	<i>Misumenops lepidus</i>	1
		Thomisidae	<i>Xysticus cunctator</i>	2
Shrubs	1	Salticidae	<i>Sassacus papenhoei</i>	2
	2	Theridiidae	<i>Theridion neomexicanum</i>	1
	3	Philodromidae	<i>Philodromus histrio</i>	3
	4	Thomisidae	—	—
Ground	1	Lycosidae	<i>Schizocosa wasatchensis</i>	1
	2	Gnaphosidae	<i>Drassyllus nannellus</i>	3
	3	Thomisidae	<i>Xysticus montanensis</i>	2

Table 3.—Horn's (1966) Index of Overlap pairwise comparisons of species level spider assemblages in vertical strata and four study plots within the sagebrush steppe at Green Canyon, Cache Co., Utah. 100% overlap is identity; 85% or greater is considered "similar".

Strata	% Overlap		
Herbs: Shrubs	73.1		
Herbs: Ground	17.7		
Shrubs: Ground	17.4		
Strata within Plots:			
Plots	% Overlap in Herbs	% Overlap in Shrubs	% Overlap on Ground
1: 2	90.4	91.9	82.3
1: 3	90.2	89.1	85.9
1: 4	84.3	88.0	79.2
2: 3	95.9	93.6	94.5
2: 4	90.8	93.6	84.0
3: 4	90.6	90.7	85.6

the ground in the present study. Hatley (1978) did not find this species above the ground at Green Canyon. I feel certain that Robinson's *Xysticus* was actually *X. cunctator*, which both Hatley and I collected in abundance on foliage; the latter identification was verified by W. J. Gertsch.] Previous authors have also found ground spider faunas to be distinct from those of vegetation (Turnbull 1973, Chaplin 1976, Culin and Rust 1980). This is thought to reflect a discontinuity between microclimates of the ground and vegetation (Elliott 1930, Gibson 1949, Turnbull 1960). Riechert and Tracy (1975) demonstrated that temperature can restrict ground spider activity, while Gertsch and Riechert (1976) considered that temperature stress is probably negligible for spiders inhabiting shrubs and tops of grass clumps.

In summary, the most important factor causing vertical stratification of spiders in the sagebrush steppe seems to be differential availability of appropriate substrate for foraging or web-building. However, effects of vegetation on spider distributions cannot entirely be separated from those of microclimate (Turnbull 1973), because plant cover greatly modifies microclimate (Geiger 1965).

Effects of Vegetation on Spiders of the Four Study Plots.—Similar plant communities have characteristic spider faunas (Barnes and Barnes 1955, Berry 1970); different plant communities have different associations of spiders (Muma 1973, Gertsch and Riechert 1976). Within a coniferous forest in northeastern Minnesota, Stratton, Uetz and Dillery (1979) found significant differences in spider families present on three tree species. One would therefore expect differences in vegetation within the sagebrush steppe to be paralleled by changes in the spider fauna. Differences in vegetation among the four study plots of the present study are described in Table 4.

Differences in spider assemblages (Table 5) were observed where vegetation differed among the four study plots. ANOVA on number of spiders in the plots was significant at $P = 0.01$ or less for each stratum. Numbers of spiders in dominant families of each stratum were significantly different among plots except for Lycosidae and Theridiidae. However, pairwise comparisons of plots for spider assemblages of strata showed overlap to be generally high (Table 3). Differences in distributions of spider foraging strategies

among the study plots were not as great as differences among strata (Figure 4). Habitat separation in sagebrush spiders seems to be more vertical than horizontal at this gross level of analysis.

HERB STRATUM. Three measures of herb stratum habitat diversity correlated with spider species richness: herb height class diversity ($r = 0.95$), herb height class evenness ($r = 0.98$), and herb species diversity ($r = 0.98$). The importance of physical structure and heterogeneity of the environment to spider distributions has been amply documented (Curtis and Morton 1974, Colebourn 1974, Gertsch and Riechert 1976, Muhlenberg et al. 1977, Lubin 1978, Uetz 1979, Hatley and MacMahon 1980, Robinson 1981).

In the present study Plot 1 provided the most diverse and abundant substrate for spiders in the herb stratum (Table 4). This was correlated with the highest spider species richness, diversity and evenness of any plot (Table 5). High diversity of herb species and cover classes, coupled with low cover class evenness, resulted in some large unispecies patches of herbs. Sampling these patches probably reduced the mean number of spider species per sample in Plot 1. Plot 2 generally had intermediate vegetational characteristics and an intermediately abundant foliage spider fauna (Table 5).

Although having generally intermediate substrate diversity, Plot 3 had the highest number of spiders and species per sample. This may have been the result of low grass density. Number of spiders in the herb stratum of each plot was negatively correlated to grass density in that plot ($r = 0.98$). Muma and Muma (1949) found grass to be a poor substrate for web spiders, and Lowrie (1968) suggested that flexible, non-woody vegetation provided unsuitable substrate for large wandering spiders. In the present study, webspinners of the herb stratum were significantly least abundant in Plot 1 (which has

Table 4.—Characteristics of the plant community in four study plots at Green Canyon, Cache Co., Utah.

Vegetation Characteristic	PLOT			
	1	2	3	4
<i>Artemisia tridentata</i>				
density (#/m ²)	0.09	0.12	0.18	0.93
$\bar{x}$ height (cm)	73.2	68.2	63.8	37.3
$\bar{x}$ cover	3552	8780	3103	670
# height classes	5	6	7	4
height class diversity	1.415	1.574	1.687	1.184
<i>Herbaceous vegetation</i>				
species diversity (H [†])	2.002	1.532	1.527	1.266
evenness (J [†])	0.589	0.496	0.458	0.457
# species (s)	30	22	28	16
density (#/m ²)	1022	1313	1248	2022
density of ground carpet ¹	557	865	893	1626
density of grass	428	421	290	388
% herbs over 25 cm tall	27.4	16.7	10.8	1.7
cover class diversity	1.142	1.197	0.913	1.036
cover class evenness	0.637	0.668	0.567	0.644
height class diversity	0.873	0.590	0.397	0.089
height class evenness	0.630	0.426	0.361	0.081

¹*Erodium cicutarium* and *Alyssum alyssoides*. See "Study Area".

Table 5.—Characteristics of the spider community in four study plots at Green Canyon, Cache Co., Utah.

Stratum	PLOT			
	1	2	3	4
HERBS				
# 100-sweep samples	131	116	105	106
# spiders collected	1503	1557	2083	1490
$\bar{x}$ spiders/sample	11.5	13.4	19.8	14.1
$\bar{x}$ species/sample	5.2	5.4	6.7	5.1
diversity (H')	2.661	2.497	2.522	2.501
evenness (J')	0.684	0.648	0.659	0.678
# species (s)	49	47	46	40
SHRUBS				
# shrubs sampled	93	89	86	86
# spiders collected	926	824	819	305
$\bar{x}$ spiders/shrub	10.0	9.3	9.5	3.5
$\bar{x}$ species/shrub	3.8	3.8	4.1	2.1
diversity (H')	2.585	2.519	2.625	2.530
evenness (J')	0.675	0.709	0.712	0.730
# species (s)	46	35	40	32
GROUND				
# trap-hours	13,619	3517	3193	2000
# spiders collected	659	325	376	231
$\bar{x}$ spiders/100 trap-hours	7.8	12.8	13.2	15.4
$\bar{x}$ species/100 trap-hours	1.5	0.9	1.0	1.3
diversity (H')	2.327	1.948	2.038	2.190
evenness (J')	0.615	0.630	0.619	0.689
# species (s)	44	22	27	24

the highest grass density); wanderers and ambushers of the herb stratum were significantly most abundant in Plot 3 (which had the lowest grass density).

In addition to its flexibility, grass presents an essentially vertical substrate, which may be unsuitable for small web-spinning spiders which prefer complex substrate (Hatley and MacMahon 1980, Robinson 1981). In the present study Dictynidae and Araneidae were least abundant where grass was most dense.

Plot 4 provided the sparsest, shortest and least diverse herb stratum and had the lowest spider species richness and low spider species diversity, but an intermediate number of spiders per sample in herbs. The latter may have been due to the low density of grass.

SHRUB STRATUM. Number of spiders per shrub was correlated to size of shrub, but coefficients of determination (r^2) were low (height = 0.31, cover = 0.40, volume = 0.31, all three = 0.43). The large shrub size in Plot 1 probably contributed to the highest number of spiders and species per shrub being in that plot. Chaplin (1976) found a correlation between shrub volume and spider numbers. Hatley (1978) suggested that larger shrubs are more diverse habitats and so should contain more species of spiders. Robinson (1981) found that numbers of spiders increased with increasing amount of substrate in artificial habitats. Another reason for the correlation of shrub height to spider abundance might be that taller shrubs catch more immature, ballooning spiders. (Spiders collected in shrubs in the present study were 95% immature.)

The sparseness (habitat island effect) of shrubs in Plot 1 and the lack of height diversity did not seem to reduce spider species richness or diversity (Table 5). However, most shrub spiders were also found in the herb stratum (see Appendix), so that shrubs were surrounded by potential faunal source areas. The abundant herb stratum of Plot 3 may also have contributed to the highest number of species per shrub and species diversity being in that plot, but Plot 3 also had a much denser shrub stratum and the highest diversity of shrub heights (Table 4).

In spite of high shrub density in Plot 4, small shrub size and lack of shrub size diversity probably led to this plot having the lowest spider species richness, diversity and number of spiders per shrub. There were significantly fewer Salticidae and Philodromidae in shrubs of Plot 4. Hatley and MacMahon (1980) found correlation between shrub height and numbers of Philodromidae and between shrub height, cover and volume and numbers of Salticidae at Green Canyon.

GROUND STRATUM. Ground-dwelling spiders were most abundant in Plots 3 and 4, which had high densities of very short vegetation (Table 4). This ground carpet may have moderated microclimate, thus establishing a more optimal environment for ground spiders. Dryness may have limited ground spiders in Plot 1, which had significantly fewest spiders per sample. Soil permeability of each plot was the same, but the water capacity of Plot 1 was slightly lower (Erickson and Mortensen 1974). In addition, cold air drainage from the canyon should have maintained a slightly higher relative humidity on the other plots. Plot 1 was slightly removed from this drainage, on a west-facing slope, and so may have had a drier microclimate. Several important groups of ground spiders had significant correlations with relative humidity.

Rocks on the surface of Plot 1 increased habitat heterogeneity by providing retreats for ground spiders. This may explain why Plot 1 had the highest species richness, diversity and number of species per sample (Table 5). One would expect to find more ground-dwelling spiders where that stratum is structurally diverse (Williams 1959, Uetz 1979).

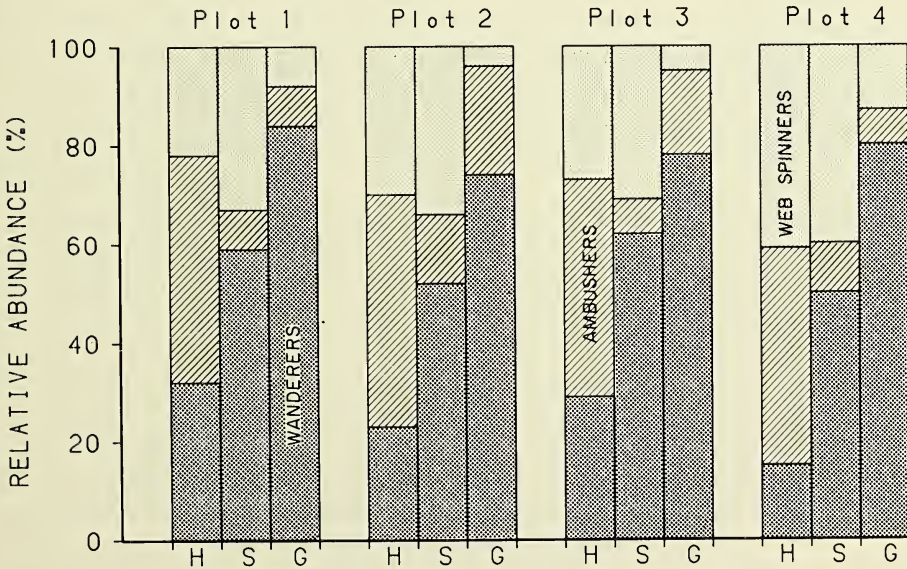


Fig. 4.—Relative abundance of three spider foraging strategies among individuals in herb, shrub and ground strata in four study plots at Green Canyon, Cache Co., Utah.

Plot 2, which was most similar to Plot 1, had few rocks on the soil surface, an intermediate number of spiders per sample, and the lowest spider species richness, diversity and number of species per sample.

Conclusions: Spatial Patterns.—The preceding discussion of spatial patterns in spider communities of the sagebrush steppe has stressed the role of substrate for spider foraging, and microclimate, which is not independent of vegetation. These seem to be the most important proximate characteristics of the environment determining spider distributions.

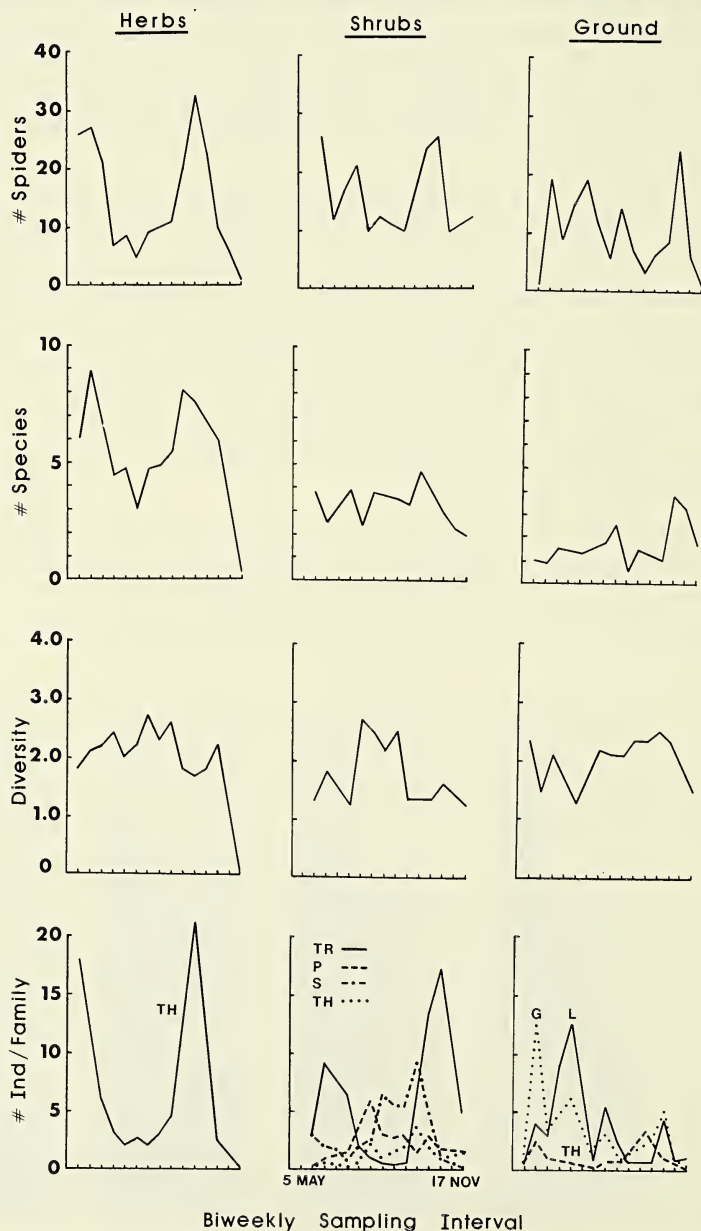


Fig. 5.—Seasonal abundance and diversity of spiders in herb, shrub and ground strata of the sagebrush steppe at Green Canyon, Cache, Co., Utah. All values are means/sample. TH = Thomisidae; TR = Theridiidae; P = Philodromidae; S = Salticidae; L = Lycosidae; G = Gnaphosidae.

Riechert and Tracy (1975) constructed a model which suggested more optimal energetics for spiders which chose the correct thermal environment rather than the environment having the most prey. Different spider foraging strategies predominate in different strata of the sagebrush steppe, due to suitability of substrate structure and microclimate. Greenquist and Rovner (1976) found differences in lycosid hunting techniques in different strata of artificial environments. Stratton, Uetz and Dillery (1979) attributed the dominance of space web spiders and orb web spiders on different coniferous tree species to substrate structure.

Nevertheless, Uetz (1977) found that weather and habitat structure were not enough to explain spider distributions. Other important elements of habitat, such as prey availability, were not evaluated in the present study. Spiders are generally considered to be polyphagous predators (Turner and Polis 1979, Olive 1980, Nyffeler and Benz 1981). Habitat characteristics favoring large numbers of spiders should also favor large numbers of suitable prey (other small arthropods). For example, Uetz (1979) found significant increases in prey species richness with increases in litter depth.

Temporal Patterns.—SEASON. In the herb stratum, spider abundance and species richness showed a spring peak followed by a summer decline, an autumn peak and a final decline to nearly zero by the end of November (Figure 5). The same abundance pattern was shown over the three years of the study and in all four study plots (Figure 6). This pattern was significant for the dominant spider family in the community (Figure 5).

MacMahon and Trigg (1972), working in the herb stratum of an Ohio old field, also found early and late season peaks in spider abundance. They attributed this pattern to phenology, rather than seasonal change in species composition of the spider community such as that which Evans and Murdoch (1968) found in adult insects of a Michigan old field.

Abundance patterns of spiders through the season may be explained as follows. Addition of individuals and species in spring was due to gradual emergence of overwintering spiders. Peak spring abundance was partly due to reproduction by spiders which had overwintered as adults or penultimate instars. The decline in number of spider species, as well as individuals, captured during midsummer suggest that phenology alone does not account for the observed pattern (Figure 5). The summer decrease in herb spider and species abundances may have been due to (1) mortality during the hot, dry part of the year (figure 2), (2) dormancy to avoid heat or water stress, or (3) dispersal out of the herb stratum or the area.

Although during June decreasing herb spider abundance coincides with increasing ground spider abundance, the latter is explained by large numbers of immature Lycosidae being captured on the ground at this time (Figure 5). The present study provides no evidence for aestivation on the ground by herb stratum spiders during the hot part of the summer.

The June decrease in herb stratum spiders also coincide with an increase in shrub stratum spiders which was not due to reproduction of the latter (Figure 5). This may indicate movement of spiders out of herbs into shrubs during the hottest part of the summer (Figure 2). Within shrubs temperature extremes are moderated. While shrub stratum spider abundance increased late in June, diversity decreased. This may have been caused by many Thomisidae moving into shrubs at this time (Figure 5).

Dispersal of juvenile spiders after spring reproduction would certainly decrease numbers of herbs stratum spiders, but probably as many spiders dispersed into the study area as out of it. The present study cannot determine whether net emigration accounted for the low summer abundance of spiders in the herb stratum.

Spring and summer peaks in ground spider abundance were each due to a significant peak in a dominant ground spider family—Gnaphosidae in May and Lycosidae in June (Figure 5). Autumn peaks in foliage spider abundance were due to reproduction by Thomisidae in herbs and Theridiidae in shrubs (Figure 5).

The winter decline in foliage spider abundance was undoubtedly due to spider migration out of vegetation to overwintering sites on the ground (Elliott 1930, Moulder and Reichle 1972). Ground spider abundance peaked simultaneously due to this influx from other strata. At the same time number of spider species was also decreasing in vegetation

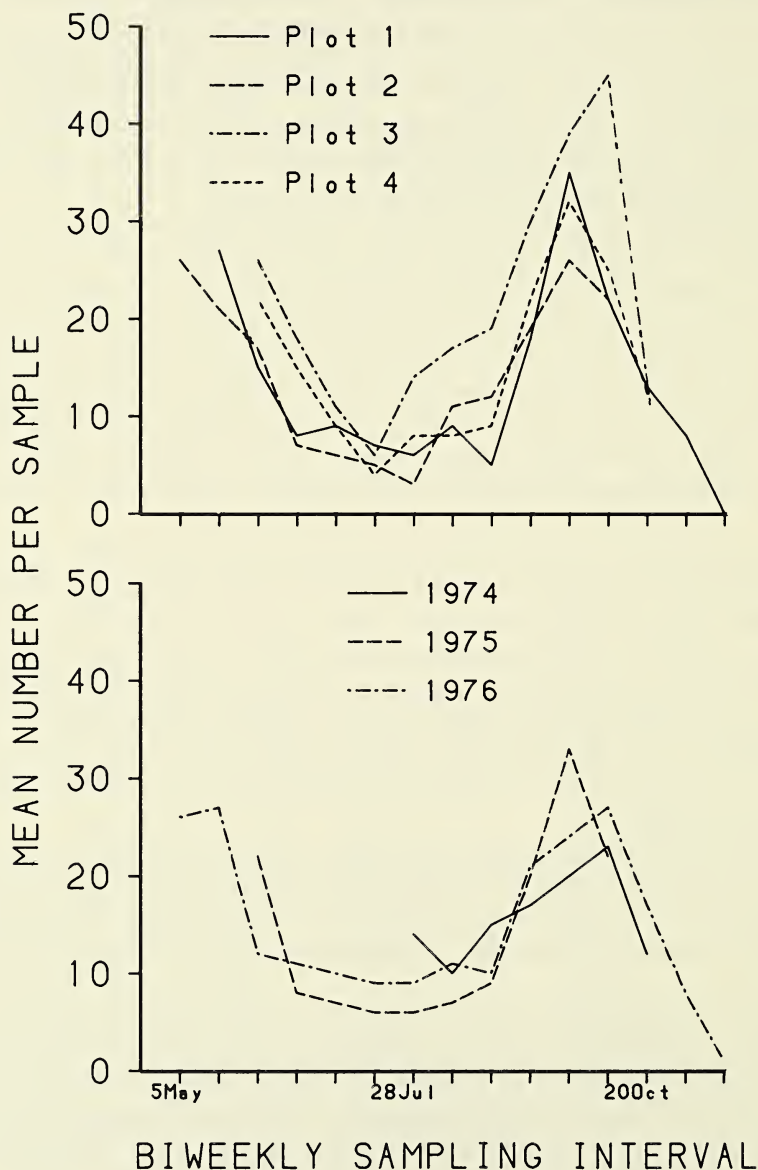


Fig. 6.—Seasonal abundance of herb stratum spiders in four study plots and three study years at Green Canyon, Cache Co., Utah.

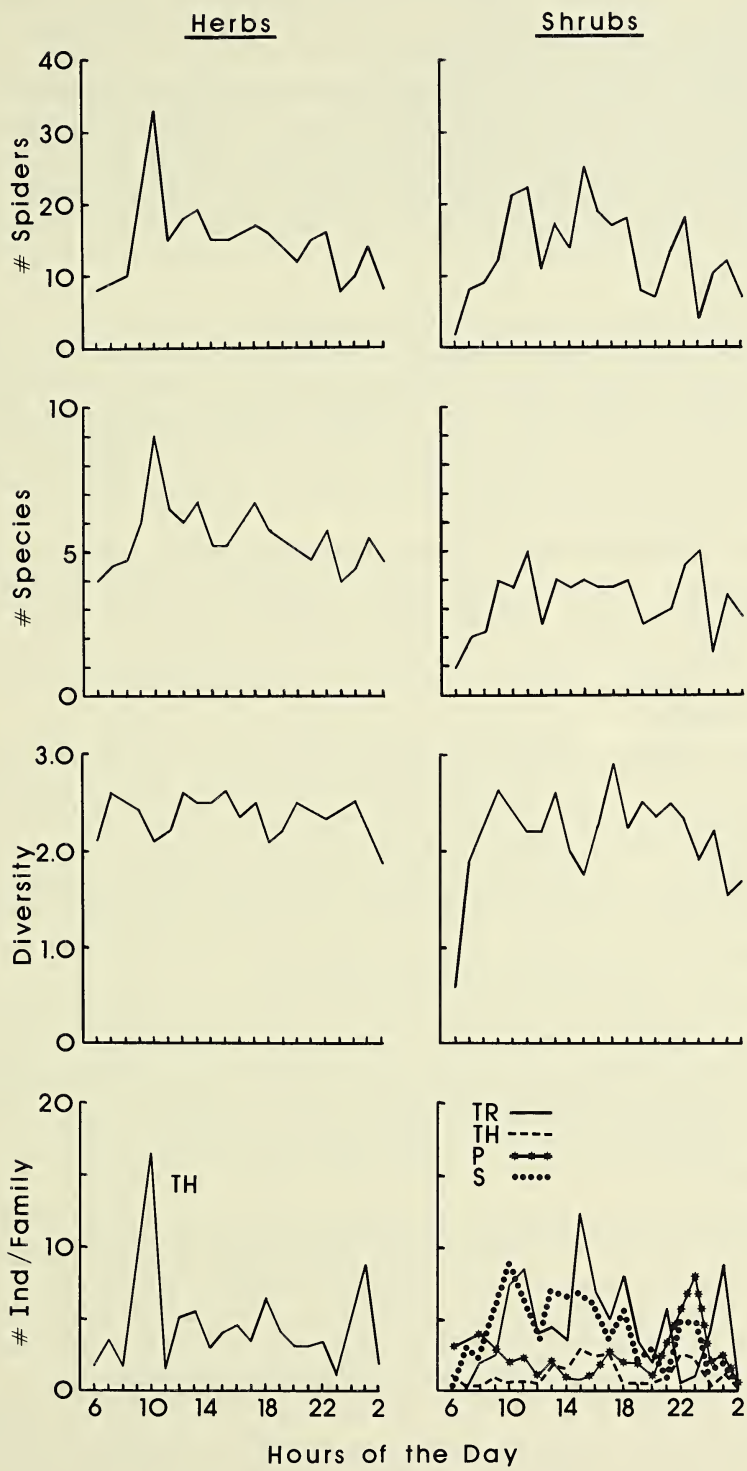


Fig. 7.—Abundance and diversity of herb and shrub stratum spiders through the day at Green Canyon, Cache Co., Utah. TH = Thomisidae; TR = Theridiidae; P = Philodromidae; S = Salticidae.

and increasing on the ground (Figure 5). The final decline in pitfall captures reflects winter inactivity. Captures of spiders on the ground began to decline when mean bi-weekly temperature fell below 5°C (Figure 2).

Species diversity of herb stratum spiders followed a pattern generally opposite to that of abundance, except for the winter decline (Figure 5). Hatley and MacMahon (1980) found a midseason peak in shrub spider diversity at Green Canyon. Although the seasonal diversity pattern shown by shrub spiders in the present study does not entirely match the above patterns, only a few shrubs were sampled during the apparent summer decline in diversity (Figure 5). If the data point for 30 June is low, these patterns would all match closely.

TIME OF DAY. Mean number of spiders per sample in herbs exhibited a significant peak at 1000 hr (Figure 7). Spider abundance was negatively correlated (linear regression) with hours of the day from 1000 to 0200 hr ($P = 0.01$, $r = -0.72$) and positively correlated from 0600 to 1000 hr ($P = 0.05$, $r = 0.90$). Although Thomisidae were collected most frequently at 1000 hr in herbs (Figure 7), this peak was not significant. Significant peak abundance of web spiders collected at this time probably made the total spider abundance curve significant at 1000 hr.

Correlations with microclimatic variables indicate that spider responses to light intensity, temperature and relative humidity interact to produce peak abundance in the herb stratum during late morning. At that time light intensity is high, but temperature is still lower and relative humidity higher than at similar light intensities in the afternoon. Light intensity was positively correlated to abundance of all important herb spider families except Philodromidae.

Abundance of spiders in shrubs was not correlated to time of day (Figure 7). This may have been due to the known moderating effect of shrubs upon microclimate allowing spiders to remain in the shrub stratum throughout the day. It may also have been due to the large number of web spiders in shrubs remaining in webs or retreats rather than migrating to another stratum to spend their inactive periods. A third possibility is dominance in shrubs being shared by families which were correlated positively (Theridiidae) and negatively (Philodromidae; $P = 0.001$) to light intensity. Philodromidae was collected significantly most often in shrubs at 2300 hr (Figure 7).

Lowrie (1971) cautioned that time of collection does not necessarily indicate time of spider activity. However, at least in the case of spiders with retreats, sampling would surely dislodge fewer inactive than active individuals (if activity affected sampling at all). The early morning dip in shrub spider diversity (Figure 7) may have resulted from collection of only species not in retreats. In herbs, spider species diversity did not vary as much through the day.

Conclusions: Temporal Patterns.—The phenology of herb stratum spiders of the sagebrush steppe seems to be adapted to avoid the hot, dry part of the year, with reproduction in the spring, the fall, or both. Some ground spiders, however, reproduce during the summer. Within each stratum, peak abundances of the several dominant families are offset (Figure 5). Ultimate factors such as competition between dominant families may play a part in this observed seasonal separation of reproductive periods.

Microclimate seems to be the most important proximate factor determining herb stratum spider abundance through the day. A more stable microclimate through the day, migration of spiders into shrubs, or competitive interactions, could result in the lack of correlation of shrub stratum spiders with time of day.

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Appendix.—Numbers and relative abundances (RA) of spider taxa collected from vertical strata of the sagebrush steppe at Green Canyon, Cache Co., Utah. Families are listed alphabetically under foraging strategies.

Spider Taxon	Herbs		STRATUM Shrubs		Ground	
	#	RA	#	RA	#	RA
Ambushers	2997	45.2	281	9.8	285	17.9
Antrodiaetidae	0	0.0	0	0.0	30	1.9
<i>Antrodiaetus montanus</i> (Chamberlin & Ivie)	0	0.0	0	0.0	30	1.9
Mimetidae	5	0.1	0	0.0	1	0.1
<i>Mimetes atkinus</i> Chamberlin & Ivie	5	0.1	0	0.0	1	0.1
Thomisidae	2992	45.1	281	9.8	254	16.0
<i>Misumenops asperatus</i> (Hentz)	41	0.6	3	0.1	0	0.0
<i>M. lepidus</i> (Thorell)	2062	31.1	158	5.5	5	0.3
<i>Xysticus cunctator</i> Thorell	872	13.2	118	4.1	62	3.9
<i>X. gulosus</i> Keyserling	16	0.2	0	0.0	13	0.8
<i>X. montanensis</i> Keyserling	1	0.0	2	0.1	174	10.9
Wanderers	1665	25.1	1638	57.0	1102	69.3
Anyphaenidae	51	0.8	33	1.2	5	0.3
<i>Anyphaena pacifica</i> Banks ¹	51	0.8	33	1.2	5	0.3
Clubionidae	46	0.7	47	1.6	93	5.8
<i>Castianeira occidens</i> Reiskind	0	0.0	0	0.0	57	3.6
<i>Chiracanthium inclusum</i> (Hentz)	46	0.7	47	1.6	2	0.1
<i>Phrurotimpus alarius</i> (Hentz)	0	0.0	0	0.0	33	2.1
Unidentified	0	0.0	0	0.0	1	0.1
Gnaphosidae	7	0.1	15	0.5	409	25.7
<i>Drassodes saccatus</i> (Emerton)	1	0.0	0	0.0	9	0.6
<i>Drassyllus insularis</i> (Banks)	0	0.0	0	0.0	51	3.2
<i>D. nannellus</i> Chamberlin & Gertsch	0	0.0	1	0.0	165	10.4
<i>Gnaphosa sericata</i> (L. Koch)	0	0.0	0	0.0	30	1.9
<i>Haplodrassus signifer</i> (C. L. Koch)	3	0.0	0	0.0	105	6.6
<i>Herpyllus</i> sp.	1	0.0	6	0.2	0	0.0
<i>Micaria</i> sp. nov.	2	0.0	7	0.2	17	1.1
<i>Nodocion rufithoracica</i> (Worley)	0	0.0	0	0.0	3	0.2
<i>Poecilochroa montana</i> Emerton	0	0.0	0	0.0	1	0.1
<i>Zelotes subterraneus</i> (C. L. Koch)	0	0.0	1	0.0	27	1.7
Unidentified	0	0.0	0	0.0	1	0.1
Lycosidae	6	0.1	1	0.0	545	34.3
<i>Alopecosa kochi</i> (Keyserling)	0	0.0	0	0.0	13	0.8
<i>Lycosa</i> sp. ¹	0	0.0	0	0.0	1	0.1
<i>Pardosa wyuta</i> Gertsch	0	0.0	1	0.0	5	0.3
<i>Schizocosa wasatchensis</i> Chamberlin & Ivie	6	0.1	0	0.0	526	33.1
Oxyopidae	50	0.8	120	4.2	1	0.1
<i>Oxyopes scalaris</i> (Hentz)	50	0.8	120	4.2	1	0.1
Philodromidae	845	12.7	508	17.7	23	1.4
<i>Ebo evansae</i> Saur & Platnick	0	0.0	3	0.1	0	0.0
<i>E.</i> sp.	5	0.1	35	1.2	0	0.0
<i>Philodromus californicus</i> Keyserling	9	0.1	1	0.0	1	0.1
<i>P. histrio</i> (Latreille)	435	6.6	307	10.7	5	0.3
<i>P. satullus</i> Keyserling	4	0.1	20	0.7	0	0.0
<i>P. speciosus</i> Gertsch ¹	1	0.0	18	0.6	0	0.0
<i>P. rufus</i> Walckenaer	3	0.1	3	0.1	0	0.0
<i>Thanatus formicinus</i> (Clerck)	33	0.5	28	1.0	15	0.9
<i>Tibellus chamberlini</i> Gertsch	135	2.0	18	0.6	0	0.0
<i>T. oblongus</i> (Walckenaer)	220	3.3	75	2.6	2	0.1

Salticidae	660	10.0	914	31.8	26	1.6
<i>Icius similis</i> Banks	1	0.0	0	0.0	0	0.0
<i>Metaphidippus aeneolus</i> (Curtis)	122	1.8	144	5.0	0	0.0
<i>M. verecundus</i> (Chamberlin & Gertsch)	14	0.2	18	0.6	0	0.0
<i>M. sp.</i>	26	0.4	7	0.2	0	0.0
<i>Pellenes hirsutus</i> (Peckham & Peckham)	50	0.8	7	0.2	6	0.4
<i>Phidippus johnsoni</i> (Peckham & Peckham)	122	1.8	54	1.9	1	0.1
<i>P. octopunctatus</i> (Peckham & Peckham)	1	0.0	1	0.0	9	0.6
<i>Sassacus papenhoei</i> (Peckham & Peckham)	277	4.2	520	18.1	0	0.0
<i>Synagales sp. nov.</i>	44	0.7	157	5.5	0	0.0
<i>Talanera minuta</i> Banks	1	0.0	0	0.0	10	0.6
Unidentified	2	0.0	6	0.2	0	0.0
Webspinners	1971	29.7	955	33.2	204	12.8
Agelenidae	0	0.0	0	0.0	46	2.9
<i>Cicurina intermedia</i> Chamberlin & Ivie	0	0.0	0	0.0	46	2.9
Amaurobiidae	0	0.0	0	0.0	4	0.2
<i>Titanoeca nigrella</i> (Chamberlin)	0	0.0	0	0.0	4	0.2
Araneidae	634	9.6	56	2.0	1	0.1
<i>Aculepeira verae</i> Chamberlin & Ivie	130	2.0	12	0.4	0	0.0
<i>Araneus gemma</i> (McCook)	15	0.2	2	0.1	0	0.0
<i>Araniella displicata</i> (Hentz)	29	0.4	1	0.0	0	0.0
<i>Argiope trifasciata</i> (Forsk.)	43	0.6	9	0.3	1	0.1
<i>Hyposinga singaeformis</i> (Schaeffer)	19	0.3	7	0.2	0	0.0
<i>Larinia borealis</i> Banks	8	0.1	0	0.0	0	0.0
<i>Metepeira foxi</i> Gertsch & Ivie	389	5.9	24	0.8	0	0.0
<i>Neoscona arabesca</i> Walckenaer	1	0.0	1	0.0	0	0.0
Dicynidae	356	5.4	35	1.2	0	0.0
<i>Dictyna completa</i> Chamberlin & Gertsch	173	2.6	22	0.8	0	0.0
<i>D. idahoana</i> Chamberlin & Ivie	182	2.7	11	0.4	0	0.0
Unidentified	0	0.0	1	0.0	0	0.0
Unidentified	1	0.0	1	0.0	0	0.0
Linyphiidae	388	5.8	68	2.4	87	5.5
<i>Erigone dentosa</i> O. Pickard-Cambridge	345	5.2	56	2.0	13	0.8
<i>Frontinella communis</i> (Hentz)	2	0.0	0	0.0	5	0.3
<i>Meioneta sp. 1</i>	16	0.2	6	0.2	18	1.1
<i>M. sp. 2</i>	0	0.0	1	0.0	1	0.1
<i>M. sp. 3</i>	1	0.0	1	0.0	3	0.2
<i>Spirembolus mundus</i> Chamberlin & Ivie	21	0.3	4	0.1	43	2.7
Unidentified	1	0.0	0	0.0	0	0.0
Unidentified	2	0.0	0	0.0	3	0.2
Unidentified	0	0.0	0	0.0	1	0.1
Pholcidae	0	0.0	0	0.0	13	0.8
<i>Psilochorus utahensis</i> Chamberlin	0	0.0	0	0.0	13	0.8
Tetragnathidae	19	0.3	3	0.1	0	0.0
<i>Tetragnatha laboriosa</i> (Hentz)	19	0.3	3	0.1	0	0.0
Theridiidae	574	8.6	793	27.6	53	3.3
<i>Dipoena tibalis</i> Banks ¹	11	0.2	22	0.8	0	0.0
<i>Enoplognatha ovata</i> (Clerck)	8	0.1	3	0.1	0	0.0
<i>Euryopis scriptipes</i> Banks	9	0.1	4	0.1	0	0.0
<i>Latrodectus hesperus</i> Chamberlin & Ivie	49	0.7	1	0.0	43	2.7
<i>Steatoda americana</i> (Emerton)	30	0.4	3	0.1	6	0.4
<i>Theridion albidum</i> Banks	2	0.0	0	0.0	0	0.0
<i>T. neomexicanum</i> Banks	460	6.9	715	24.9	3	0.2
<i>T. petraeum</i> L. Koch + <i>T. rabuni</i> Chamberlin & Ivie ²	5	0.1	45	1.6	1	0.1

1) Probable identification (—W. J. Gertsch)

2) Author unable to separate species (majority immatures)

THE BIOLOGY OF *OCTONOBA OCTONARIUS* (MUMA) (ARANEAE, ULOBORIDAE)

Juanita E. Peaslee

Rt. 1, Box 17
Centerview, Missouri 64019
and

William B. Peck

Biology Department
Central Missouri State University
Warrenburg, Missouri 64093

ABSTRACT

The biology of *Octonoba octonarius* (Muma) was studied over a two year period of laboratory rearing and field observations. Under laboratory conditions the spider matured as a fifth or sixth instar. First nymphal instars still in the egg sac fed upon uneclosed eggs and second prelarvae. Web construction and nutritive behaviors followed patterns recorded in the Uloboridae. Courtship and mating patterns differed from others of the family in that typically two serial copulations were followed by immediate sperm induction and two additional brief copulations. A chalcid, *Arachnopteromalus dasys* Gordh, newly described from specimens found in this study, whose larva is an egg predator, *Achaearanea tepidariorum* (C. L. Koch), and man's activities were the principal ecological pressures on *O. octonarius* populations.

INTRODUCTION

Although there is an abundance of information concerning the habits of the various Uloboridae (Kaston 1948, Gertsch 1949, Bristowe 1939, 1958, Millot 1949, Savory 1952, Marples 1962, Szlep 1961, Eberhard, 1970, 1971, 1972, 1973, 1976), specific studies of *Octonoba octonarius* (Muma) (sub *Uloborus octonarius*) have not been reported other than when it was described by Muma in 1945, in the revision of the Uloboridae by Muma and Gertsch (1964), and by Opell (1979). Wilson (1969) considered *O. octonarius* in his study of the spinning apparatus of spiders, and Eberhard (1971) mentioned that this spider is unsuitable for laboratory experiments in web building because the species seems to be unable to produce normal webs consistently under laboratory conditions. This study, then, is an attempt to deal with the biology and life history of *Octonoba octonarius* as observed in a large population inhabiting a grain elevator in Johnson County, Missouri, and in the laboratory.

MATERIALS AND METHODS

Specimens were initially collected in a grain elevator in Warrensburg, Missouri, during the months of June and July and observed in the laboratory for two years. Field observations of the spider and an egg predator associated with it were conducted in the elevator, in a barn, and in a basement.

Dixie cups of about 90 ml capacity were used as rearing containers, inverted on convenient-sized plywood pieces which could be stacked. The cups provided an effective attachment surface for web building by the young spiders and were suitable for microscopic examination of the specimens and the web. For observations of web construction and maintenance, of feeding, and of interactions between adults and between the adult female and young, various containers were used.

The spiders were fed principally on *Drosophila melanogaster* three to five times a week. Individual spiders were fed by dropping live prey onto the web. To reduce web damage by the prey, injured flies were fed to young spiders. Young spiders were offered one injured fly per feeding, and the adults received one or more flies depending on the availability of prey and its acceptance. Insects of suitable size other than *Drosophila* were offered to the adults when available. Prey remains were removed at the following feeding.

Penultimate or younger males and females from field and laboratory stock were isolated prior to their final molt in preparation for courtship, mating, and sperm induction studies. Virgin females were placed in an observation chamber and allowed time to construct a web before a male was introduced. The male was placed either in the bottom of the container and allowed to find his way upward or was placed on the web as far away from the female as possible in order that he might adjust to new surroundings before interacting with the female. The courtship, mating, and sperm induction sequences were observed with and without the microscope and were also recorded on film.

Embryonal development was studied in field-collected egg cases and those constructed in the laboratory. Eleven egg cases 4-24 hours old were teased open and the eggs counted and measured with a micrometer. Some of the eggs were placed in Stender dishes and immersed in oil, a technique developed by Holm (1940), which renders the chorion transparent and allows for the observation of the developing embryo. Another group of eggs was placed in a Stender dish and allowed to develop in a high humidity incubator. Laboratory conditions of temperature and light were variable. The development of the embryos was observed daily except during the periods of most rapid change when observations were made every six hours.

Observations of stadal development were made on 113 individuals obtained from two egg cases made by a field-collected female which had matured and mated in the laboratory, and nine individuals obtained from two cases made in the field and hatched in the laboratory. The dates of molting, width of the carapace at the time of molting (Dondale 1961), chaetotaxy, and any changes in pigmentation were observed and recorded for each individual. Exuvia were removed after each molt.

Feeding and courtship behaviors were filmed thus enabling us to analyze the rapid movements of the spider which could not be followed by the eye. Transparent acrylic plastic cubes 8 cm x 8 cm with removable ends were constructed for filming these activities (Figure 1). The acrylic plastic allowed filming through the container from various angles with minimum glare. Masking tape 2 mm wide was placed in the cube as shown to provide a better attachment surface for the silk and to influence a more uniform placement of the webs within the cube.

RESULTS AND DISCUSSION

Although the genus *Octonoba* is principally tropical (Opell 1979), *O. octonarius* has been recorded in the United States from Maryland and South Carolina to north-central Texas and eastern Kansas. As is typical in all of its range, the spider has been found in barns, other buildings, and in basements in west-central Missouri: Warrensburg, Johnson County, 1968 (W. B. Peck); Centerview, Johnson County, June 1973 (J. Peaslee); June 1974 (Jani and Gary Colster); Holden, Johnson County, September 1974 (Jason Behm); Stockton, Cedar County, September 1975 (J. Peaslee). New records include Massachusetts, Middleboro, Plymouth County, July 1977 (J. Peaslee); and Indiana, St. Meinrad Abby, Spencer County, July 1978 (J. Peaslee).

Developmental Biology.—The study of the life history of a spider must consider the embryonal development for a complete picture of the stages in its life cycle. However,

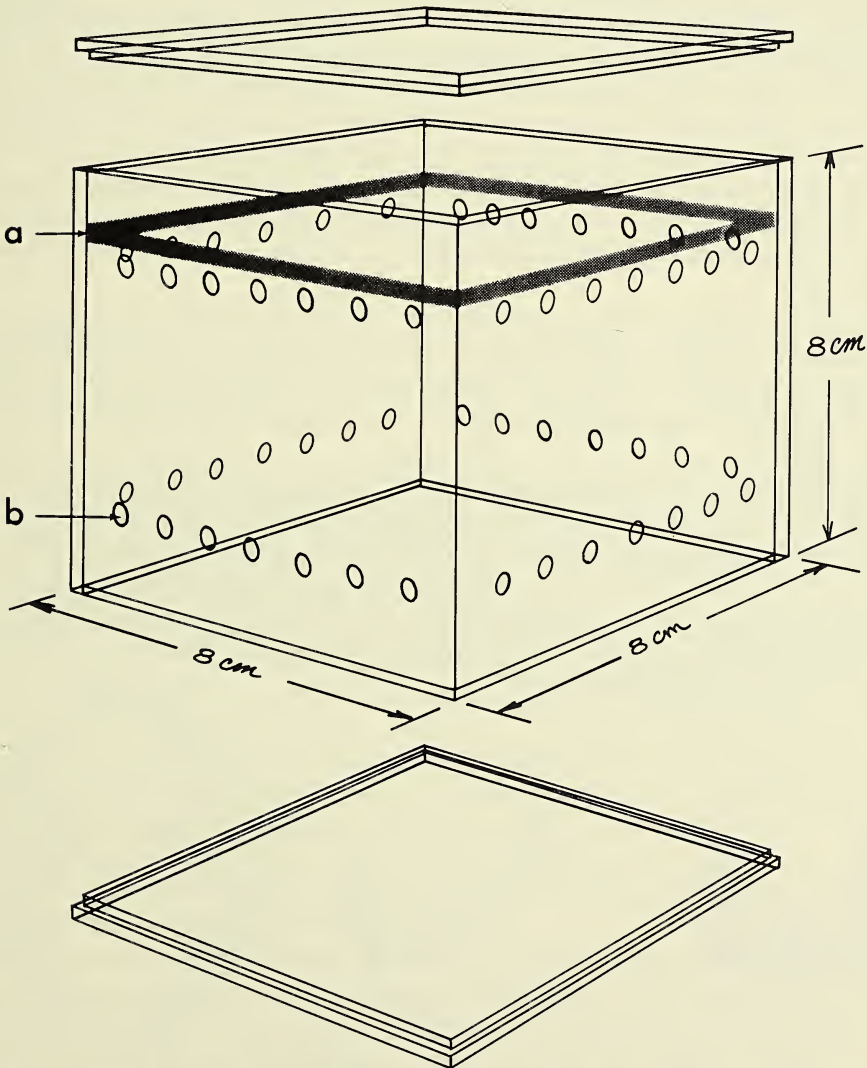


Fig. 1.—Container for viewing and filming courtship and feeding behaviors: a, tape for control of web placement; b, holes for ventilation.

confusion of terminology in the literature has impaired facile discussion of the developmental stages. Recent comparisons and clarifications of the various systems of nomenclature of the developmental stages were made by Galiano (1969), Peck and Whitcomb (1970), Valerio (1974), Hydorn (1977), and Whitcomb (1978).

In this discussion, the outer egg membrane is called the chorion, the inner egg membrane carrying the egg teeth is termed the vitelline membrane, and the interior embryonic membrane, the third membrane (Galiano 1969). Eclosion refers to the rupture and sloughing of the chorion. Ecdysis designates a true molt, that is, the shedding of an integument that is not an egg membrane. Ecdysis occurs as the larva molts to the first active instar and in all the succeeding molts. Vachon's terminology (1957), which designates the developing stadia before the first true molt as first prelarva, second prelarva, and larva, is utilized. The first prelarva refers to the embryo enclosed in the chorion with cephalothorax and abdomen in planes at right angles to each other. The second prelarva refers to the embryo enclosed in the vitelline and third membranes and with body parts still in two planes. Larva is the term used to designate the stadium free of embryonic membranes, having a transparent integument, and having the cephalothorax and abdomen in the same plane. While recognizing the validity of the terms nymphal instar as used by Vachon to refer to the immature stages after the first true molt, Kaston (1970) and Schick (1972), among others, adopted the convention of referring to the immature nymphal stages simply as the first instar, second instar, etc. This convention is used here with the understanding that the number of the instar refers only to "post-embryonal" or nymphal stadia and that the preceding stages, first prelarva, second prelarva and larva, are "embryonal."

Immersed in oil, the first apparent change in the embryo of *O. octonarius* occurred approximately 32 hours after oviposition, when a concentration of blastodermal material appeared as an opaque plate in one area of the egg. Ultimately this concentration of material formed the germ band that appeared as a ridge and from which further development occurred.

The appendages were evident at approximately 76 hours after oviposition, appearing as small buds. By 144 hours the buds had elongated, become folded ventrally across the embryo, and showed some evidence of segmentation. By approximately 192 hours (8 days), the egg teeth (Holm 1940), had developed at the base of the chelicerae in the clypeal area (Figure 2), and the embryo could be seen as a two-part body with segmentation evident on the abdomen. The contours of the chorion reflected the changes that were occurring beneath the membrane.

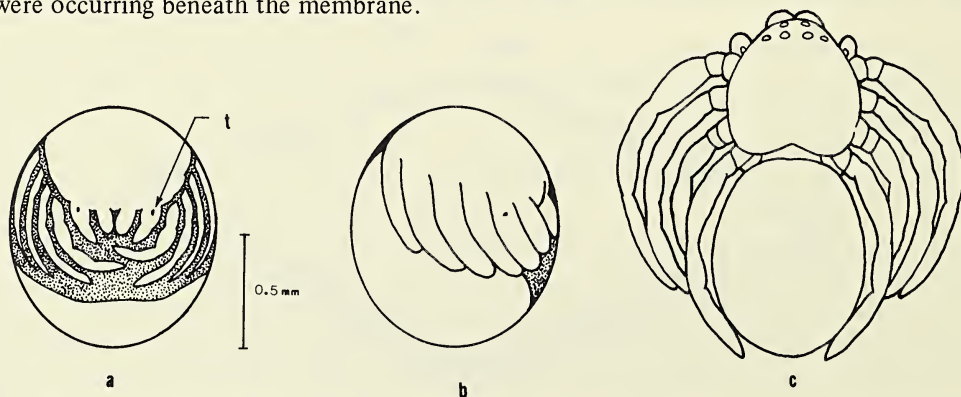


Fig. 2.—Embryo and larva of *O. octonarius*: a, first prelarva showing egg teeth (arrow); b, lateral view, first prelarva; c, larva after casting embryonic membranes.

Table I.—Mean time in days from oviposition to: Eclosion, Second Prelarva, Larva, and First Nymphal stadium of four broods of *O. octonarius* collected from field sites. Numerals in columns refer to numbers of individuals.

Stage of	Days									
	10	11	12	13	14	15	16	17	18	Mean
Eclosion										
Brood G	7	2								
Brood E		2	19							
Brood S		4								
Brood R		1								11.3
Second Prelarva										
Brood G		6								
Brood E			20							
Brood S			4							
Brood R			1							11.8
Larva										
Brood G		5	1							
Brood E			1	20						
Brood S				4						
Brood R				1						12.6
First Nymphal										
Brood G							6			
Brood E								8	13	
Brood S										
Brood R							1			17.2

External changes in the eggs that were not immersed in the oil could first be detected as white dots on the chorion that corresponded with the appendage buds. Changing contours on the chorion could be seen as the appendages developed and folded ventrally, and as it reflected the two-part shape of the embryo.

Eclosion occurred about 80 hours after the appearance of the egg teeth or approximately 270 hours (12 days) after oviposition (Table 1). The egg teeth pierced the chorion, and an intermittent, pulsating movement began in the clypeal area and spread posteriorly. The pulsations gradually increased in frequency until the chorion parted abruptly at point near and including one of the projecting egg teeth. About 24 minutes after the onset of eclosion, the carapace and legs were freed, and the wrinkled membranes collected at the caudal tip of the abdomen. The vitelline membrane was cast about 10 hours after eclosion in the same manner as the chorion. The technique of Galiano (1969) of marking each membrane as it was cast, provided evidence that the third membrane was cast simultaneously with the vitelline membrane.

After the casting of the vitelline and third membranes, the abdomen and the prosoma assumed a monoplanar position, and the larva became more spider-like (Figure 2c). The appendages extended stiffly from the body and were segmented except at the tarsal-metatarsal articulation. The appendages moved with strong flailing motions, but the organism was not ambulatory. It could not right itself when on its back and was unable to grasp anything. The caudal mass of embryonal membranes was cast completely. The only pigmentation was that of the red, rudimentary eye spots.

The larval stage lasted from 24-36 hours, during which period the flailing activity continued. Segmentation of the appendages progressed, and the spinnerets became better defined. Setae developing under the larval integument gave the appearance of cuticular pigmentation first on the sternum and later on the cephalothorax and abdomen. Ultimately a longitudinal black striping on the appendages, resulting from the appression of setae by the integument, signaled the imminence of ecdysis.

Ecdysis occurred about 17 days after oviposition. The nymphal cuticle was transparent with numerous black setae, but within 24 hours the body had become black except for white spots on the abdomen (Figure 3a). The legs, except for leg IV which had dark bands on the patellae, tibiae, and metatarsi (Figure 3e), remained pale. The first instar spiderlings were ambulatory and very active; and those that were removed from the egg sac were capable of spinning a simple (not hackle-band) type of silk. Some of them constructed an irregular web. They emerged from the egg sac 2-3 days after ecdysis. They lacked a calamistrum (Figure 3b) and cribellum, but within 24-36 hours after emergence from the egg sac, they were able to construct a "primary type" web. (See Webs)

While still in the egg sac, the first instar spiderlings were observed to feed on uneclosed eggs and on prelarvae, a phenomenon that has been recorded in *Phidippus* (Taylor and Peck 1975), *Latrodectus* (Kaston 1970), *Achaearanea* (Valerio 1974), *Misumenops* (Schick 1972), and *Chiracanthium* (Peck and Whitcomb 1970, Mansour et al. 1980). Cannibalism was not observed inside the cocoon, but when the young spiders were kept from dispersing, within 12 hours after their emergence they would attack, capture and wrap siblings.

Unaided by the female, spiderlings emerged from cocoons made in the laboratory by field-collected females 20 days after oviposition. The web of the adult served as a substrate for the young spiders as they emerged, as avenues for traveling, or as attachment spots for their own webs. Before they constructed their own web, the first instar spiders in the adult's web fed on prey that was not attacked by the female.

Octonoba octonarius molted to the second instar from 20-55 days after the first ecdysis (Figure 4). This contrasted with *Uloborus walckenaerius* Latreille and *Uloborus plumipes* Emerton that molted four and six days respectively after emergence from the egg sac (Szlep 1961). The second instar *O. octonarius* had a cribellum and a calamistrum of widely spaced setae (Figure 3d), and constructed an orb web of hackle-band silk. It also acquired a row of five or six setae retrolaterally placed on tarsus IV (Figure 3d), which increased to 12 to 16 in succeeding instars. This comb-like row of setae appears to function in spreading silk in prey wrapping or other silk-spinning activities not associated with web construction.

Maturity was usually reached in the fifth or sixth stadium. The duration of the stadia varied greatly among individuals, as noted by Szlep (1961), especially after the second instar. The first and second stadia ranged in time from 7-55 days and the later stadia from about 15 to as many as 215 days. Color changed from black to shades of brown, the dorsum and venter acquired the irregular dark brown pattern characteristic of the species (Figure 5), and the dark bands on tibiae I gradually darkened and enlarged. Changes in chaetotaxy were principally evident in the number and refinement of the setae of the calamistrum and the comb-like row of macrosetae on tarsi IV. At the final molt, the female, and especially the male, acquired several macrosetae (Figure 6).

Mortality was high in the laboratory especially in the first three stadia. About 13% of the young survived to the fourth instar and about 4% to maturity. Szlep (1961) and Turnbull (1965) believed lack of food to be a factor in the high mortality in the early

instars. In the laboratory, inability to construct adequate webs, a prerequisite to prey capture, seemed largely responsible for food deprivation in early stadia. Incomplete ecdysis, or deformed appendages were also major causes of death in later stadia.

Courtship and Mating.—After initial recognition signals and responses of web vibration and tarsal contacts, a courtship pattern begins and may be repeated as many as fifty times before copulation is accomplished. The male advances toward the female, typically in her orb web, and touches her with his first tarsi (Figure 7a). Then usually both, but invariably the male, turn and move away from each other. The male, as he turns, attaches a strand of silk below the orb and retreats 3-4 cm (Figure 7b). This strand corresponds to the "mating thread" referred to by Platnick (1971) as typical of orb-building species and by Whitcomb and Eason (1965) in their study of *Peucetia viridans* (Hentz). The male then turns back toward the female, attaches the newly spun strand again, and moves toward her, spinning a dragline as he goes. About mid-distance on his return he cuts the mating thread he has just made (Figure 7d). The portion of the mating thread that is behind him is held with his fourth pair of legs and the portion ahead of him is held with the second and third pairs of legs (Figures 7e). Holding both portions of the severed thread, he makes

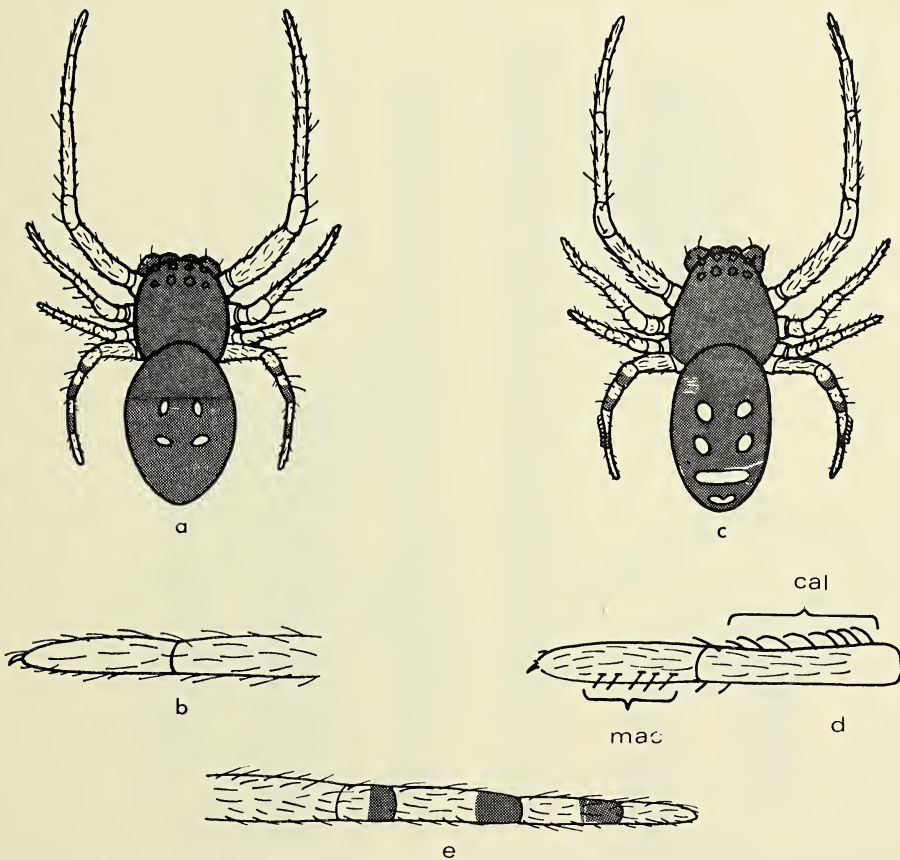


Fig. 3.—First and second instar *O. octonarius*. The body of the spider in both instars is black with white spots: a, first instar; b, first instar metatarsus and tibia IV without calamistrum or row of macrosetae; c, second instar; d, second instar metatarsus and tibia IV with calamistrum and macrosetae; e, leg IV pattern, first and second instar.

10-12 rapid strokes on the forward portion. The female, who is typically positioned with her abdomen toward the male, responds by turning quickly, attaching a dragline, and grasping the thread held by the male with her legs II and III. With a series of stroking motions initiated by the male, first on the mating thread, then on the fore legs of the female, the two move closer together.

In close contact they begin to lower themselves below the orb, venter to venter, on separate strands of dragline silk, grappling with their legs as they descend. During these actions, the thread originally held by the male was released and the pair maintained physical contact with their legs (Figure 7f). Abruptly the female retracts legs II, III, and IV upward and flattens them posteriorly against her abdomen. The male grasps the anterior surfaces of the female's first femora and maintains a brief, stable contact (Figure 7g). He then extends a palp and, using his hold on the female's front legs as a lever, springs forward, clasps the legs of the female to her body with his legs II, III, and IV, and applies a palp to the female's epigynum. The pair remains *in copula* about 1-1.5 minutes. A movement of the legs of the female is a signal for the two to spring apart, each then

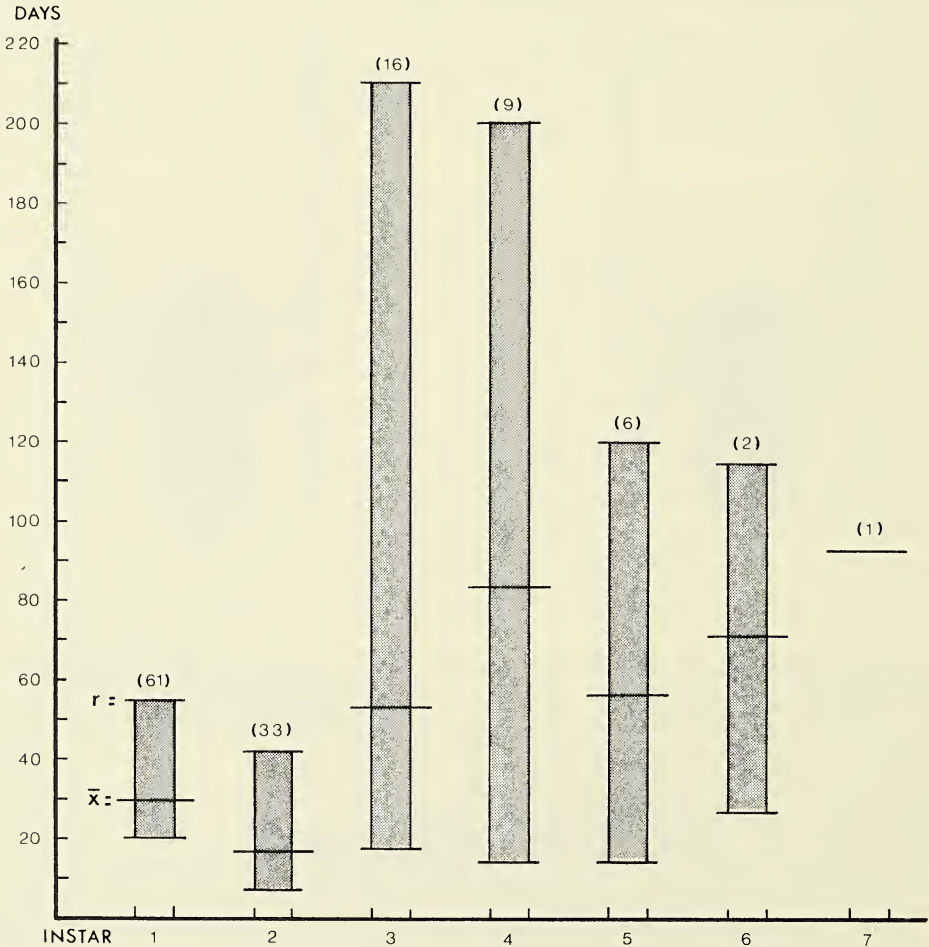


Fig. 4.—Range and mean duration in days of stadia of *O. octonarius*. Numbers in parentheses are numbers of individuals.

hanging from its respective silk line. Each then typically grooms plapi and legs while hanging from the lines or after moving to separate parts of the web.

The preliminary approach may occur many times before a successful clasp is achieved. One pair, both of which were collected in the penultimate stadium and matured in the laboratory, accomplished a successful clasp only after 45-50 pre-clasp patterns. The critical time in the pattern seems to be during the sparring and lowering sequence. If responses are not correct at this time, the sequence is broken and the male typically starts

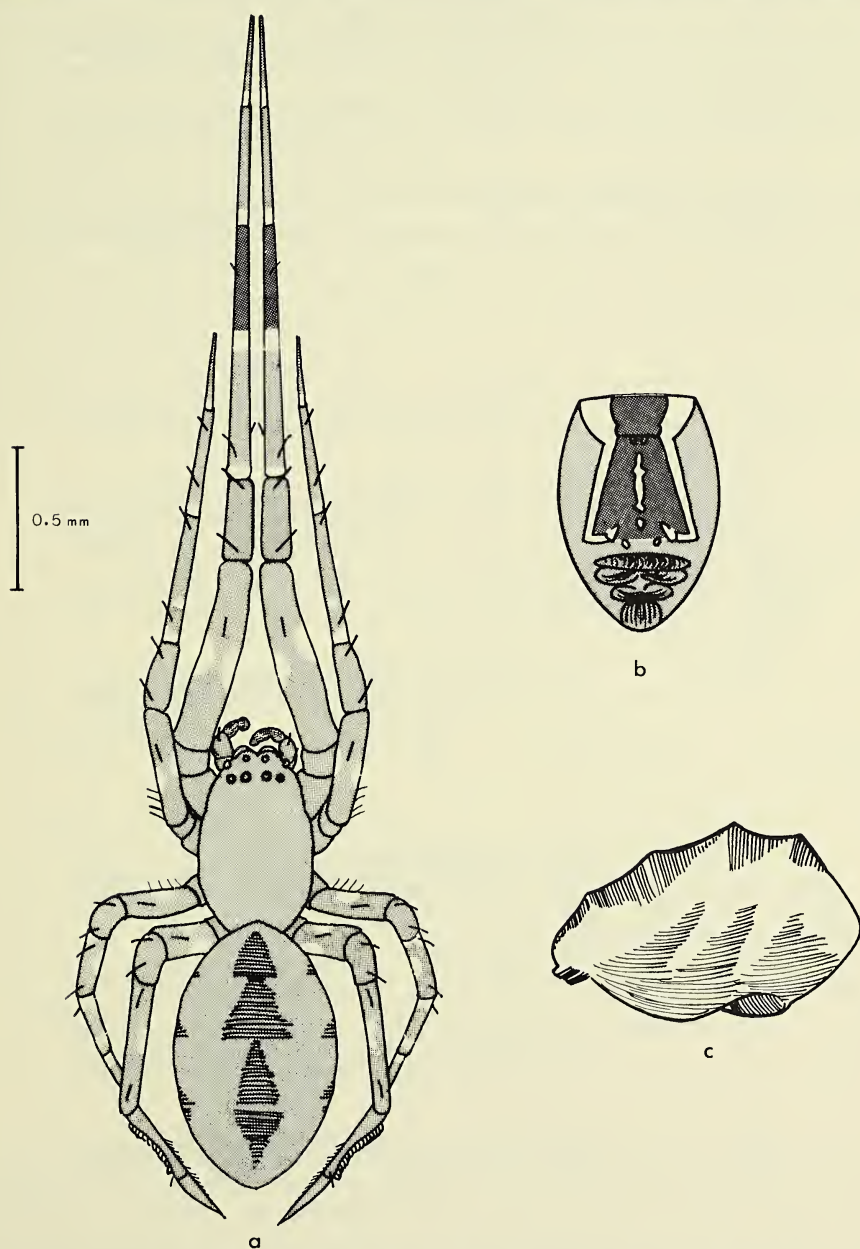


Fig. 5.—*Octonoba octonarius*: a, color pattern of adult female; b, color pattern of venter of adult female; c, lateral view of dorsum of adult female showing diagnostic humps.

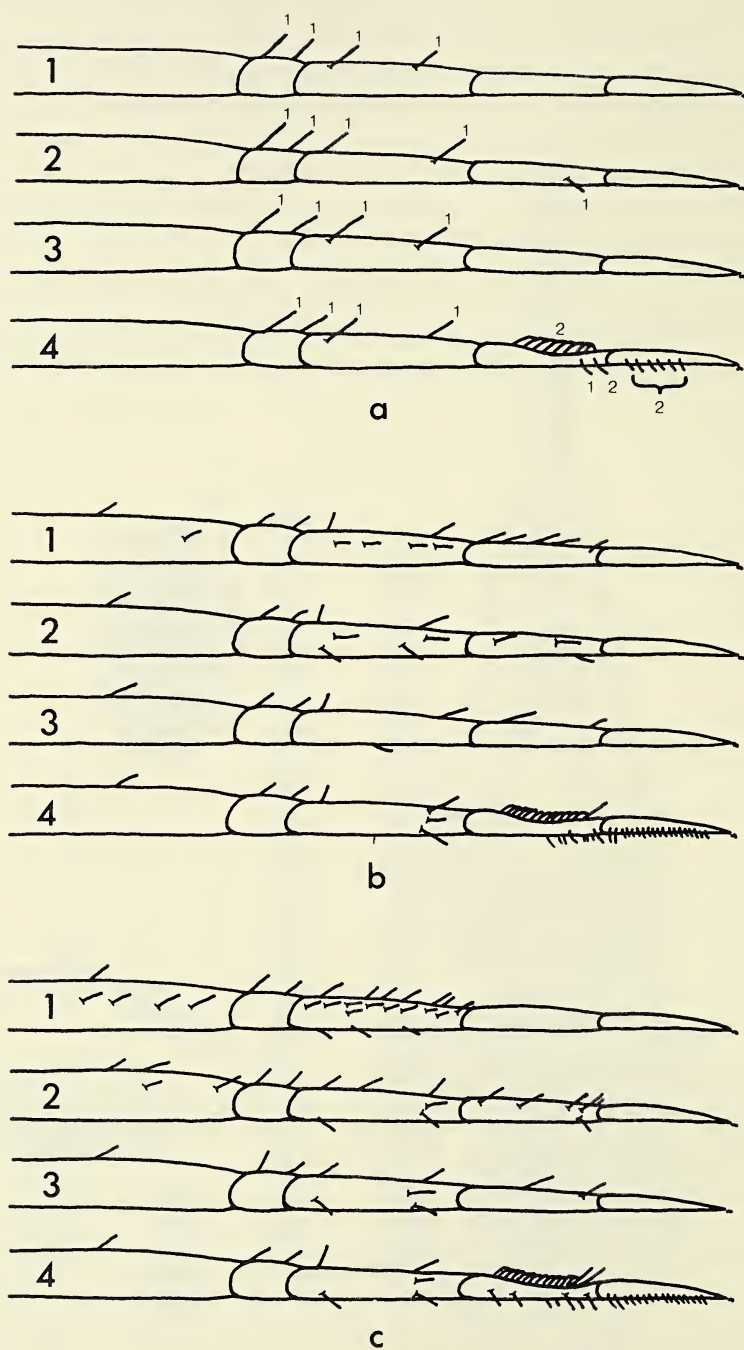


Fig. 6.—Changes in macrosetae on legs of *O. octonarius*. (1 and 2, prolateral views of legs I and II; 3 and 4, retrolateral views of legs III and IV); a, first and second instars (small numerals designate instar); b, adult female; c, adult male.

the entire pattern again. Although nine of the ten pairs observed required several attempts to attain the clasp, one pair, a female that had matured in the laboratory about a month before and a newly collected, mature male, completed the entire courtship and mating sequence without repeating any of the pre-clasp pattern. After a successful copulation, the courtship pattern is usually repeated until a second sequence of successfully completed.

After a second copulation, the male typically retires to the side of the orb and constructs a sperm web, which is a triangular-shaped supporting structure about 1 cm long supporting a "puff" of silk. With his back legs he gathers the puff under his abdomen, turns his body sideways to the puff and moves to the top of the sperm web. There he raises his abdomen for about 5 seconds and deposits seminal fluid on the puff. He then moves under the web to recharge his palpi, and after about 30 seconds under the sperm web, he typically returns to the female's web.

With palpi recharged, the male executes complete courtship patterns again until he accomplishes two more successful copulations. The second copulation is much briefer, lasting less than 30 seconds. Following them, the male grooms and either leaves the web or retires to its periphery. (One male started a third sperm web before leaving the female's web.) The female typically returns to the center of her web. Analysis of the sequence was possible only after filming the process.

Although Rovner (1967), for *Linyphia triangularis* (Clerck), and Gregg (1967), for *Ixeuticus* reported interruptions in copulation for sperm induction, immediate additional

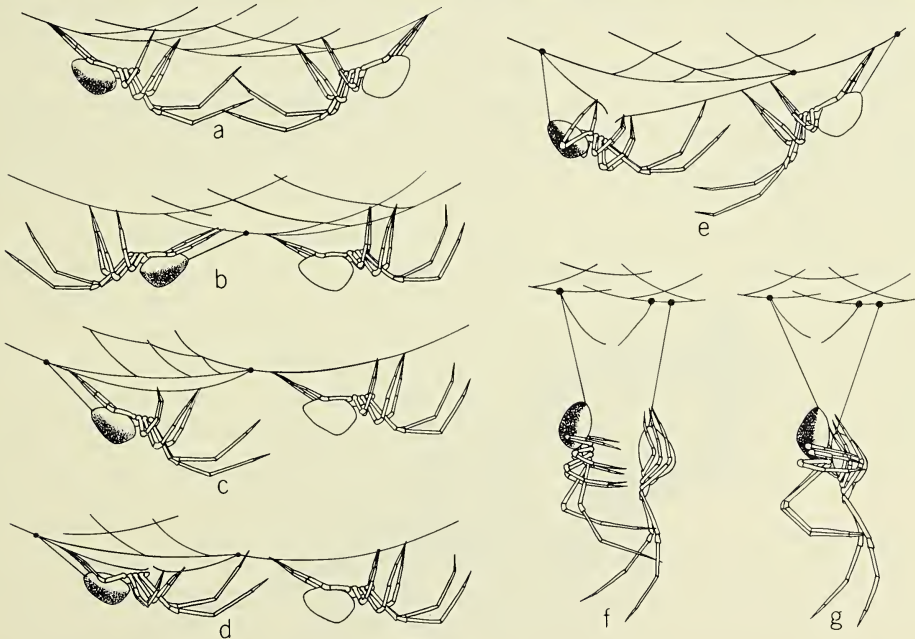


Fig. 7.—Diagrammatic sequence of the courtship and copulation of *O. octonarius*. The male is represented by the darkened figure. a, both touch tarsi; b, both turn away, male begins construction of silk strand, the mating strand, beneath female's web; c, male pivots 180 degrees back toward female on mating strand; d, male cuts mating strand and holds severed strands taut with legs II, III, and IV, strokes taut strand nearest female with legs I; e, female turns, exchanges strokes, and both advance toward each other; f, both descend on separate lines, female retracts legs, male holds legs I of female with his legs I; g, using his grip on female's legs as leverage, the male springs forward to clasp female.

copulations were not reported in uloborids. Bristowe (1958) reported that the male of *U. walckenaerius* inserted each palp once for about 5 minutes each before the pair parted, which differs considerably from the much briefer, interrupted pattern observed in *O. octonarius*.

Females seldom attack the males before or after courtship. On one occasion after mating, a male caught and began to wrap a fly, which was confiscated by the female; and the male backed off unharmed.

In the laboratory, females were receptive to mating only once. Males would mate with several females.

Egg Sacs.—Egg sac construction and oviposition occur at night and require approximately 3 hours. The upper covering of the egg sac is constructed first with the female holding on to the web with her two anterior pairs of legs and moving her abdomen back and forth attaching essentially parallel strands of silk. The tarsi of the posterior legs are used to press the silk strands more firmly together, giving the forming fabric a smoother and more compact texture than is evident in the fluffly, newly extruded silk. Silk is deposited and compressed on both the upper and lower surfaces of the fabric as the spider changes position, adding layers to the disc. The upper covering is completed in about 15 minutes and eggs are extruded onto its under surface upon its completion. Eggs are laid in a viscid matrix that adheres to the upper cover as described by Gertsch (1949) in *Argiope* and by Whitcomb et al. (1967) in *Oxyopes*. The bottom cover is woven in the same way as the upper one and the two are joined.

Although initially constructed within it, the completed lenticular-shaped egg sac is suspended just above or below and in the same plane as the orb web. Strong silk strands attach it to radials in the outer portions of the orb.

The new sac is light brown or beige and typically changes to gray later. It is 8.4-10.6 mm long, 5.2-8.8 mm wide, and 3.5-5.3 mm thick. Its shape is generally rectangular with five to eight sharp projections at the points of attachment of the silk guy lines (Figure 8).

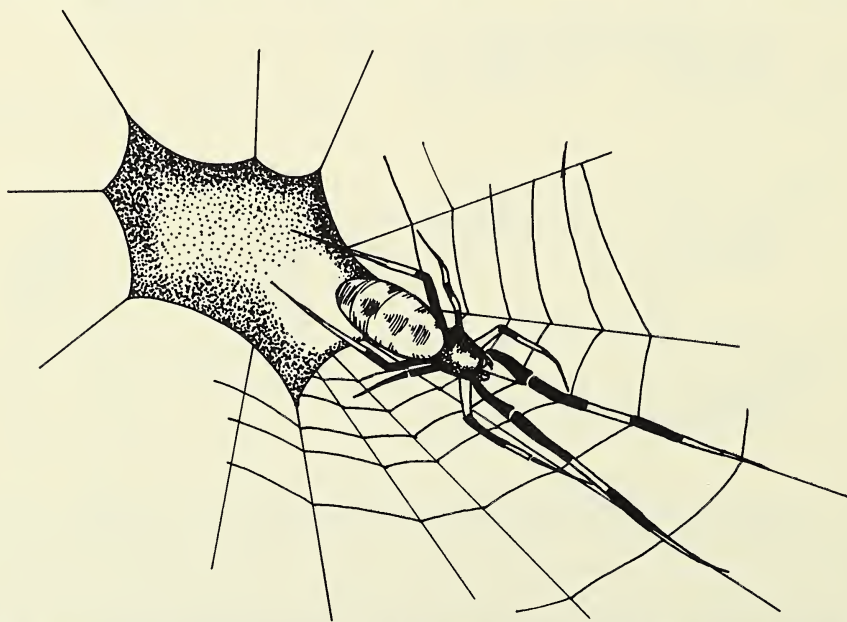


Fig. 8.—Female *O. octonarius* guarding egg sac. The female remains with her legs touching the sac for approximately 24 hours and then moves to a position near it.

After oviposition the female usually remains near the egg sac for about a day with her fourth legs touching it (Figure 8). Hentz (1850) reported this same behavior in *Uloborus glomosus* (Walckenaer) (sub *Phillyra* spp. Hentz). She withdraws gradually and after several days returns to her more typical resting location in the center of her web. Her withdrawal is so consistent that a rough estimate of the age of the egg sac can be made from this behavior.

In the laboratory, females constructed one to five cocoons ($\bar{X} = 3$). The spherical eggs were cream colored and averaged 0.7 mm in diameter. Fourteen sacs collected from field sites had 45-107 eggs per sac with a mean of 78.

Field observations indicate that oviposition occurs at two peak times, mid-June through early July and mid-August through early September. However, cocoons were found in the field as early as May 10 and as late as November 30.

Feeding Habits.—Feeding habits of the uloborids are discussed by Marples (1962), Gertsch (1949), and Opell (1979). Glatz (1970) described the manipulation of the swathed prey by the mouthparts and ingestion. *Octonoba octonarius* does not vary in significant detail from those described behavior patterns.

In the laboratory a spider often accepted a second prey while it was ingesting a previously captured one. It typically carried the wrapped prey in its palpi to the site of new activity, quickly immobilized the new prey, and then wrapped both together. Partially wrapped prey was sometimes left, and the spider returned later to consume it.

Field and laboratory observations indicated that acceptable prey include various Coleoptera, Isoptera, muscid flies, and *Drosophila*. Adult *Tribolium confusum*, although of appropriate size, was generally not accepted as prey.

Acceptable prey for adult spiders range in size from 1-2 mm to 1-2 cm, the latter being two to three times the size of the spider. The spiders tend to consume large prey at the spot where it is first immobilized rather than carry it back to the center of the web. Vigorous activity of potential prey more than prey size seems to discourage its capture.

Webs.—The cribellum and calamistrum, their silk, and the design of the orb web of uloborids have been studied extensively. Details of the web construction behavior of *O. octonarius* appear to be the same as those in *Uloborus diversus* Marx as elucidated by Eberhard (1971). As in other uloborids (Eberhard 1971), the webs of *O. octonarius* are repaired and enlarged extensively. Usually the hub area is repaired, often by constructing another sector of the orb in the damaged area. An individual frequently abandons the old web and constructs a new one alongside or at an angle to the old web, using it as a beginning point for the new one (Figure 9). Observations in the laboratory and in the field confirm that such web complexes composed of four to five webs usually belong to a single individual.

Eberhard (1971) suggested that the repaired sections in the webs of *U. diversus* are an economical means of extending the prey capture area. The older, abandoned units of the multiple webs occupied by *O. octonarius* are often dust-covered. This web may not be very efficient in prey capture but is perhaps advantageous as an early predator warning system since disturbances in any part of the web complex can be detected by the spider.

Adult females are found in three types of webs: 1) a single orb occupied by a single individual which usually represents a new web at a new site, 2) a three-dimensional web occupied by a single individual, as discussed previously, that results from patching, extending, and appending new webs to the old ones, and 3) a three-dimensional complex that results from several spiders constructing webs in close proximity with anchor lines attached to neighboring webs. On such web complexes a disturbance at one area is transmitted to other parts of the web.

In the grain elevator where most field observations were conducted, webs were concentrated around windows, in a three-story stairwell, and around machinery. Turnbull (1964) in his study of site preference by *Achaearanea* and Yoshida (1977) for *Tetragnatha* found that those spiders remained in one location as long as prey was available, and that they abandoned sites that yielded inadequate prey. Light had no bearing on site selection by *Achaearanea*, but air currents did seem to have some influence. Prey insects were more abundant near windows where *O. octonarius* webs were found. There was also better air circulation there, a factor pertinent to web construction. A combination of air currents and light probably accounted for the concentration of webs in the stairwell.

The young *O. octonarius* are capable of spinning the primary web in the first instar. A primary web, as described by Szlep (1961) and Eberhard (1971), is a web without cribellate silk or "sticky" spiral but with many additional radii. The first instar of *U. plumipes* and *U. walckenaerius* laid down additional radii over the temporary spiral instead of cribellate silk, giving the web a sheet-like appearance (Szlep 1961).

We observed primary webs constructed in the occupied webs of older spiders, presumably the maternal web. Primary webs were also found singly and in groups of 3-12 webs in different planes placed one above the other.

Immature males construct typical uloborid webs, and mature males were collected in the field in typical orb webs, but it was not determined if they were of their own making. Males never constructed orb webs in the laboratory, but they did spin irregular webs containing patches of heavy, "non-sticky" silk.

Frequently, but not consistently, a stabilimentum is added to the web of a young or adult *O. octonarius*. Stabilimenta are of three basic types: 1) a zigzag, similar to the one constructed by *Argiope*, which passes through the hub, 2) a zigzag spiraling around the hub, and 3) one with extra silk added to the hub (Figure 10). Field observations failed to

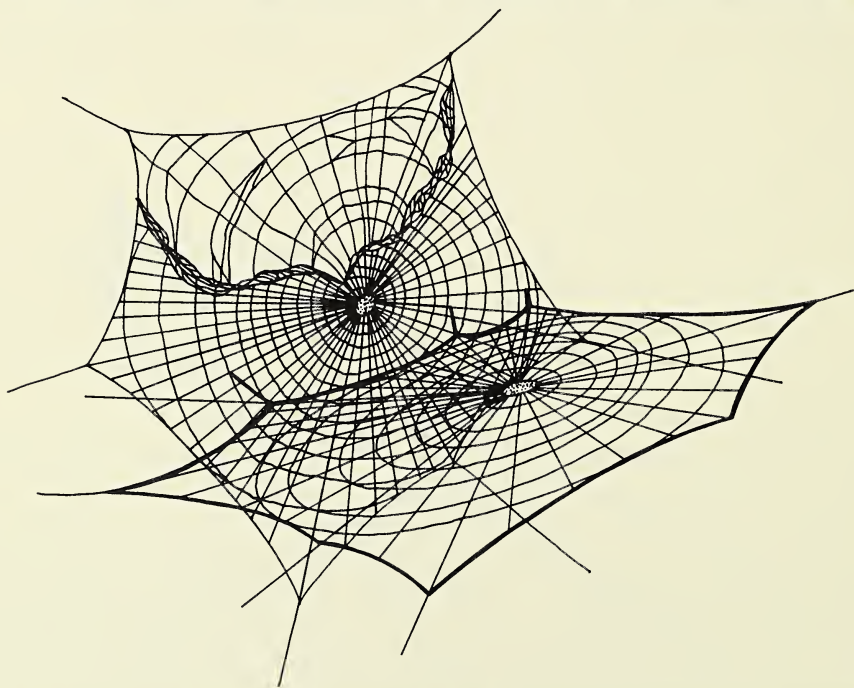


Fig. 9.—Web complex of a single *O. octonarius* female illustrating the spider's habit of repairing the web and joining another web to the original in another plane.

disclose any behavioral or abiotic factors that influenced the presence or type of structure. On some occasions few or no stabilimenta were found, and on other occasions there was a virtual "bloom" of them.

Enemies.—Except for predation by *Achaearanea tepidariorum*, a hitherto unknown chalcid, and activities of man, no other enemies of *O. octonarius* were encountered. Man's cleaning activity and his destruction of the webs that clutter the buildings they are probably the principal pressure on expanding populations. *A. tepidariorum*, which is frequently found in the same habitat, commonly feeds on adults and later instars.

Bradoo (1972) recorded an egg parasite, *Idris* sp. (Scelionidae, Hymenoptera) in an unidentified species of *Uloborus* which lives as a commensal in the webs of *Stegodyphus sarasinorum* Karsch, but no other parasites or egg predators have been reported in the Uloboridae (Auten 1925, Eason et al. 1967). Our finding of an egg predator that attacks a spider in a family which is apparently rarely "parasitized" is of some interest. *Arachnopteromalus dasys* Gordh which was described as a new genus (Gordh 1976) parasitized 78% of the egg sacs of *O. octonarius* at one field site.

A. dasys was first found in late June from the basement, and other infested egg sacs were later collected from other sites. Between 6 June and 10 September, 58% of the egg sacs collected from all field sites contained the predators. The two periods of active infestation coincide with the most active egg-laying cycles of the spider.

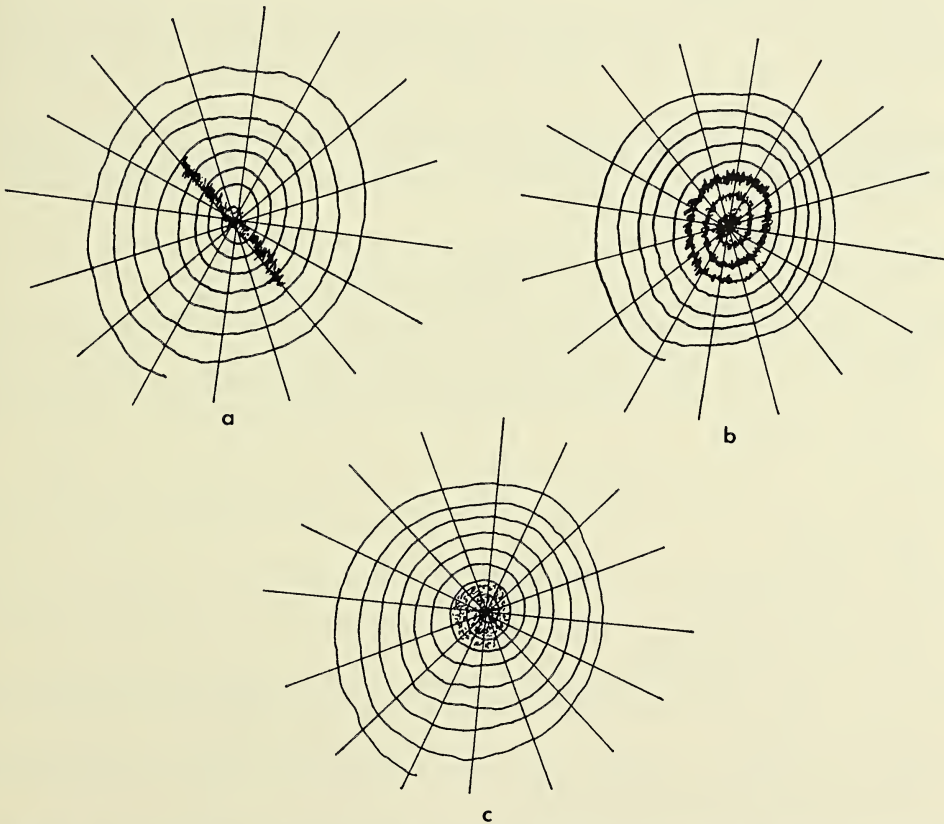


Fig. 10.—Stabilimenta constructed by immature and adult *O. octonarius*: a, zigzag strip through center; b, zigzag spiral around center; c, filled-in center.

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POST-BIRTH DEVELOPMENT OF *VAEJOVIS* *BILINEATUS* POCOCK (SCORPIONES: VAEJOVIDAE)

W. David Sissom¹ and Oscar F. Francke

Department of Biological Sciences
Texas Tech University
Lubbock, Texas 79409

ABSTRACT

The post-birth development of *Vaejovis bilineatus* Pocock was studied in the laboratory. Litter size varied from 17 to 26 among five litters reared. The average growth factor between successive molts for carapace length was 1.26 ± 0.05 ; for chela length 1.28 ± 0.05 ; and for metasomal segment V length 1.32 ± 0.07 . Although no specimens were reared from birth to maturity, it was determined by extrapolation and comparison with field-collected adults that there are six instars (five molts) to maturity.

INTRODUCTION

Only two studies dealing with post-birth development of the Vaejovidae have been published to date. Francke (1977) reared *Uroctonus mordax* Thorell in the laboratory, but only one male successfully reached the fifth instar. From its size at that age, Francke estimated that maturity was reached at the seventh instar. Polis and Farley (1979) conducted field studies on *Paruroctonus mesaensis* Stahnke. They reported that (1) maturity was reached at 19 to 24 months of age, (2) there were seven instars in the post-birth development, and (3) growth was determinate. In addition they discussed ecological parameters affecting the life history of *P. mesaensis* and presented a summary of all published scorpion life histories in tabular form.

In addition to these studies, there have been several others of related interest. McAlister (1960) discussed growth rates of first instar young of *Vaejovis spinigerus* (Wood). Williams (1969) published information on birth behavior for *Anuroctonus phaidactylus* (Wood), *Uroctonus mordax* Thorell, *Vaejovis confusus* Stahnke, *V. minimus* Kraepelin, *V. spinigerus*, *V. vorhiesi* Stahnke, and *P. mesaensis*. He also included descriptions of first and second instars of those species. Haradon (1972) published additional information on birth behavior for *U. mordax*. Finally, Hjelle (1974) published observations on the birth and post-birth behaviors of *Syntropis macrura* Kraepelin.

The present study represents the first developmental information available for the genus *Vaejovis* beyond the second instar. Five pregnant females of *Vaejovis bilineatus* Pocock were collected at Villa Hidalgo, San Luis Potosí, México in March 1977. They gave birth in the laboratory in August and their litters ($n = 17, 20, 22, 25$, and 26) were

¹Present Address: Department of General Biology; Station B, Box 1812; Vanderbilt University; Nashville, Tennessee 37235.

reared. As the litter of one female ($n = 17$) died as second instars, the specimens were omitted from all calculations. Fourteen specimens from the other litters entered the fourth instar and one of those entered the fifth. An immature female collected with the adults at Villa Hidalgo molted twice and reached maturity in the laboratory. The specimens from these two sources provided a complete study of the post-birth development of *V. bilineatus*.

MATERIALS AND METHODS

Rearing methods used in this study have been described elsewhere (Francke 1977, 1979). Briefly, young scorpions born in the laboratory were separated into individual containers as soon as the litters dispersed from the females' dorsa. A layer of soil was provided as a substrate, and water was provided with a moistened sponge. Early instars were fed macerated bits of roaches (*Nauphoeta cinerea* Saussure), as available living prey were too large for the young scorpions to subdue. The later instars were given live immature *N. cinerea*. All specimens were maintained in an environmental chamber at near constant temperature ($26.6 \pm 2^\circ\text{C}$).

Two problems resulted in loss of specimens and/or data. The macerated bits of roaches used as food molded rapidly and young scorpions became trapped in the fungal hyphae. The specimens were killed and usually damaged as a result. Other specimens died after burrowing in the soil and desiccated so that measurements were useless.

Measurements of carapace length, pedipalp chela length, and metasomal segment V length were taken for all instars observed (either from exuviae or preserved specimens). All measurements were taken with an American Optical Model 569 binocular dissecting microscope equipped with an ocular micrometer calibrated at 20X.

Growth factors between successive instars were calculated from the data by dividing the dimension of a structure at one instar by its dimension at the previous instar. An average growth factor and the standard deviation were calculated for each molt from the pooled data. In the text and tables, all average ages, measurements, and growth factors are accompanied by the standard deviation (in the form of $\bar{x} \pm s$) unless otherwise specified.

The failure of specimens to reach maturity required the use of extrapolation and calculation of 95% confidence intervals of instars not observed in the litters (see Francke 1979 for procedure). Measurements of field-collected adults from the same or nearby localities were compared to predicted size ranges of instars, and the instar at which maturity is reached was thus inferred.

RESULTS

First Instar.—The young of *Vaejovis bilineatus* are born enclosed by a "birth membrane" as are other apoikogenous scorpions (Francke, in press). Upon freeing themselves from this membrane the young climb onto the mother's dorsum and orient themselves in rows with the prosoma directed forward and the metasoma backward. This layering effect was reported by Williams (1969) for several *Vaejovis* spp. and is apparently characteristic of the genus. We have observed the same for *V. coahuilae* Williams and *V. waueri* Gertsch and Soleglad.

The first molt occurred at an age of 9.78 ± 0.41 days. Molting of all the young took place in a single day. Dispersion of the young took two to four days to complete, and this process began at an age of 16.8 ± 1.7 days (7.0 ± 1.6 days after the first molt).

First instars of *V. bilineatus* are creamy white at birth and gradually darken until time of exuviation. As in all other scorpions studied to date, they lack many adult features.

Tarsi are blunt and lack claws; the aculeus is soft and blunt; trichobothria, setae, granulation, and carinae are absent; and the denticles on the margins of the pedipalp chela fingers are absent. Pectines, however, are well developed and contain the complete number of pectinal teeth.

Second Instar.—Laboratory mortality was very high in the second instar. Only 40 of 93 specimens (43.0%) survived this stage, and most of the deaths were probably due to dessication either prior to or during molting. There is good evidence for mortality from molting difficulties: specimens dying during or around peak molting periods had formed a new cuticle which was visible underneath the semi-transparent second-instar cuticle in the carapace region.

Specimens surviving the second instar ($n = 40$) molted to the third instar at an age of 106.2 ± 15.6 days. The duration of the second instar was 96.2 ± 15.7 days (range = 68-140 days) (Table 1). Measurements of second instar structures and growth factors for the second molt are found in Table 2. Growth factor information could be obtained for only 31 of the 40 specimens: seven specimens dessicated before measurements were taken and two died during the second molt (there was no cuticular expansion and hardening). The average growth factor from second to third instar in carapace length was 1.26 ± 0.06 ; in chela length 1.28 ± 0.05 ; and in metasoma V length 1.33 ± 0.07 .

Second instars possess most of the adult characters. The body is covered with setae, and all trichobothria are present. The tarsi bear claws, the aculeus is hardened and sharp, and the dentate margins of the pedipalp chela fingers are developed. Coloration is essentially the same as in adults. Carinae of the pedipalps and metasoma are very poorly developed (carinal development is gradual throughout life).

Third Instar.—Of the 40 specimens reaching the third instar, only 14 (35%) completed it. Specimens surviving this instar molted to the fourth instar at an age of 190.1 ± 27.9 days. The duration of the third instar was 87.5 ± 20.4 days (range = 56-140 days) (Table 1). Measurements of third instar structures and growth factors for the third molt are found in Table 2. Only nine of 14 specimens yielded growth factor information: three specimens dessicated during the fourth instar (measurements were not possible) and two died during the third molt. The average growth factor from third to fourth instar in carapace length was 1.26 ± 0.04 ; in chela length 1.27 ± 0.04 ; and in metasoma V length 1.30 ± 0.04 .

Fourth and Succeeding Instars.—All remaining young except one died during the fourth instar. The surviving specimen molted to the fifth instar at an age of 323 days; the duration of its fourth instar was 147 days (Table 1). Measurements of fourth and fifth instar structures are reported in Table 2.

One immature female was collected with the pregnant females at Villa Hidalgo; it molted twice in the laboratory and attained maturity. Growth factors for this specimen did not differ from the laboratory-reared litters (Table 2). The duration of its penultimate instar was 243 days. The specimen did not molt between January 1978 and its death in October 1981, so apparently there is no post-reproductive molt in this species. This is further evidence that post-reproductive molts do not occur in the Scorpiones.

Using methods described by Francke (1979), 95% confidence intervals were calculated for the fifth, sixth, seventh, and eighth instars. These confidence intervals were calculated from measurements and growth factors of fourth instar specimens ($n = 9$), rather than from the single fifth specimen. The confidence intervals for carapace length, chela length, and metasoma V length are found in Table 2.

Table 2.—Measurements in mm and growth factors of observed instars (mean ± standard deviation); predicted 95% confidence intervals for instars not observed in the laboratory; and measurements of field-collected specimens of *Vaejovis bilineatus* Pocock.

* denotes estimated instars of collected specimens.

	Carapace	Chela	Metasoma V
OBSERVED			
2nd instar (n = 88)	1.43 ± 0.07	1.61 ± 0.08	1.34 ± 0.09
Growth factor (n = 31)	1.26 ± 0.06	1.28 ± 0.05	1.33 ± 0.07
3rd instar (n = 31)	1.86 ± 0.13	2.09 ± 0.15	1.82 ± 0.17
Growth factor (n = 9)	1.26 ± 0.04	1.27 ± 0.04	1.30 ± 0.04
4th instar (n = 9)	2.30 ± 0.13	2.58 ± 0.18	2.30 ± 0.17
Growth factor (n = 1)	1.23	1.29	1.36
5th instar (n = 1)	2.74	3.30	2.89
Female molting in laboratory			
4th instar*	2.56	2.89	2.61
Growth factor	1.23	1.26	1.33
5th instar*	3.15	3.65	3.46
Growth factor	1.29	1.34	1.27
6th instar*	4.05	4.90	4.40
PREDICTED 95% CONFIDENCE INTERVALS			
5th instar	2.57 – 3.22	2.85 – 3.75	2.54 – 3.49
6th instar	3.23 – 4.06	3.65 – 4.80	3.30 – 4.54
7th instar	4.07 – 5.12	4.67 – 6.15	4.29 – 5.90
8th instar	5.13 – 6.45	5.98 – 7.87	5.57 – 7.66
FIELD-CAUGHT SPECIMENS			
Adult females (n = 9)	3.83 ± 0.39	4.62 ± 0.30	4.14 ± 0.26
Adult males (n = 2; range)	2.98 – 3.25	3.90 – 4.10	3.55 – 3.75
4th instar* (n = 2; range)	2.40 – 2.50	3.00	2.55 – 2.60
5th instar* (n = 2; range)	2.75 – 2.85	3.30 – 3.60	2.90 – 3.40

DISCUSSION

When measurements of field-collected adults are compared to the confidence intervals obtained from the laboratory-reared litters (Table 2, Fig. 1), most of them (73%) fit easily within the intervals predicted for the sixth instar. However, three adult females (two giving birth to laboratory-reared litters and the immature specimen molting twice in the laboratory) fall within the lower limits of the seventh instar. Although it is possible that these three females are indeed seventh instars, we consider them to be large sixth instar adults based on the following observations. The young of one litter are significantly larger than the others (Duncan’s multiple range test; $\bar{x}$ ’s = 1.37, 1.41, 1.41, 1.42, 1.52; $p < 0.01$), and extrapolation from the average size of second instars (using the growth factor obtained from this litter) shows that a specimen of this litter could easily fit in the predicted seventh instar confidence intervals after only four molts. The fact that some specimens do not fit in the “correct” size range suggests limitations in the method, but this is primarily due to the difficulty in rearing large numbers of scorpions past the early instars.

Only two adult males were available for comparison. In chela and metasoma V length both specimens fit the sixth instar confidence intervals. In carapace length one specimen is slightly smaller than predicted; the other is just within the lower limit for the sixth

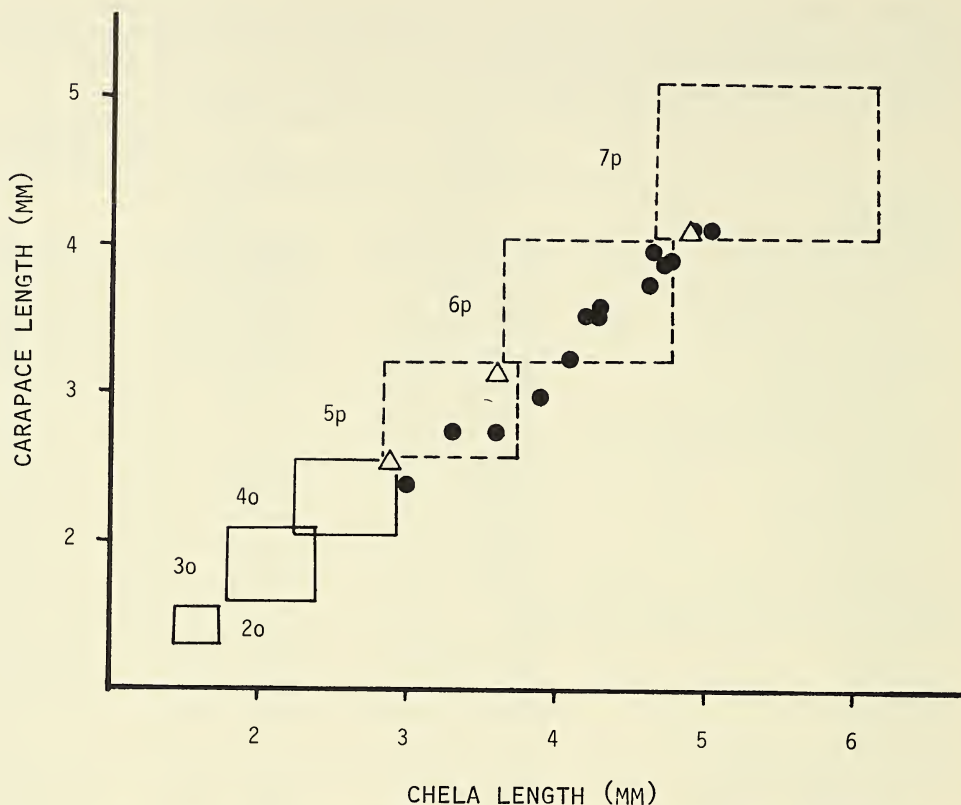


Fig. 1.—Plot of carapace length versus pedipalp chela length in instars of *Vaejovis bilineatus*. Boxes with solid lines depict 95% confidence intervals for instars observed (o) in the laboratory (2nd through 4th); boxes with broken lines depict 95% confidence intervals for predicted (p) instars (5th through 7th). Symbols are as follows: $\circ$ = field-collected specimens; $\triangle$ = exuviae and specimen of female molting to maturity in the laboratory.

instar. This could be attributable to sexual allometry, but sample sizes of both field-collected adults and laboratory-reared specimens were too small to permit statistical analyses.

As stated previously there are potential problems with estimating size ranges of instars not observed. To minimize these problems, the estimations should be derived from large sample sizes of late instars, as this reduces error considerably. Another problem encountered in using this method is that of allometric growth at the maturation molt. This is common in scorpions (e.g., allometry in the metasomal segments in male *Centruroides* spp.), but with prior knowledge of its occurrence, adjustments can be made with reasonable accuracy (Sissom and Francke, unpublished data).

Data for instar duration obtained in the laboratory probably do not reflect durations in the field, as feeding regimes certainly differ. These data are reported here as they may prove useful in future laboratory studies.

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CHEMICAL AND VIBRATORY COMMUNICATION IN THE AQUATIC PISAURID SPIDER *DOLOMEDES TRITON*

Chantal Roland¹ and Jerome S. Rovner

Department of Zoology
Ohio University
Athens, Ohio 45701

ABSTRACT

Male *Dolomedes triton* perform announcement displays consisting of leg-waving and jerks in response to water that has contacted the integument of female conspecifics. Jerks cause bursts of concentric surface waves that probably provide a signal for the female. Males also follow the female's dragline, using a lycosid-like manner on land but switching to rowing and pulling when the line is on water. When close enough to touch the female, the male performs a courtship display consisting of rapid leg tapping, which, with the female's leg-waving, results in prolonged leg interplay between the sexes.

INTRODUCTION

The role of chemical communication in various families of spiders was reviewed recently by Tietjen and Rovner (1982). Its use by pisaurid spiders was established experimentally by Kaston (1936), following earlier suggestions by Bonnet (1924) and Bristowe and Locket (1926). Carico (1973) included some comments on the probable role of chemoreception during reproduction in *Dolomedes*, while Williams (1979) examined its importance for predation in this genus.

Our present investigation centered largely on three questions about chemical communication in *Dolomedes triton* (Walckenaer): (1) Does its pheromone persist on wet surfaces and water? This is not the case in those species of the closely related lycosid spiders so far studied, in which water inactivates the substance (Dondale and Hegdekar 1973, Tietjen 1977). (2) Do male pisaurid spiders follow female draglines? Dragline-following in T-mazes has been studied in lycosids (Dijkstra 1976) and in agelenids (Krafft and Roland 1979, Roland in ms.). Following of draglines in open arenas has been examined in various lycosids (Engelhardt 1964, Richter 1972, Tietjen 1977, Tietjen and Rovner 1980). (3) Can male spiders follow female draglines on water? Our observations and experiments indicate the answer to all three questions to be "yes." In addition, we provide descriptive data on other aspects of pre-copulatory behavior in *D. triton*, including the likelihood of communication by surface waves in such aquatic spiders, previously suggested by Bristowe (1958).

¹ Present address: Université de Nancy I, Laboratoire de Biologie du Comportement, C. O. 140, 54037 Nancy-Cedex, France. (Use J. Rovner's address for reprint requests.)

GENERAL METHODS

Penultimate and adult *D. triton* were collected along the margin of Dow Lake in Athens County, Ohio, during June and July, 1981. Spiders were housed individually in plastic cages (13 X 7 X 7 cm high), each cage having a paper floor and a cotton-stoppered vial of distilled water. Mealworm larvae (*Tenebrio*) or cockroaches (*Periplaneta*) were offered two or three times weekly. Room temperature usually was 25° (range, 23°-27°). Lighting in the windowless room remained on a 12-hr light/12-hr dark cycle. We filmed behavior with a Bolex Super-8 Macrozoom 160 camera at 18 frames/sec and a Cine-8 high-speed camera (Visual Instrumentation Corp., Model SP-1) at 100 frames/sec.

Individuals providing stimuli in Experiments 1, 2, 3, and 5 were housed in glass-topped 5-gal aquaria (41 X 21 X 26 cm high), which were filled with water to a depth of 5 cm. (Since tap water was used, freshly filled aquaria stood for one day before introduction of the next resident.) A strip of wood (20 X 3.5 X 0.6 cm) placed on the water at one end of the aquarium served as a resting site for the spider, which typically remained with two or three anterior leg tarsi floating on the water. Residents were housed in their aquaria for at least two days prior to the use of these aquaria in experiments. Aquaria used to house males had never been used previously for females. (Separate brushes and jars for each sex were used when transferring spiders from one container to another.) In these experiments the aquarium resident was removed and the male introduced to the half of the water surface opposite that containing the resting site. Thus, males were never placed initially at the location where the resident spent most of its time and never were placed in an aquarium that simultaneously contained another spider during these tests for responsiveness to potential chemical stimuli.

DESCRIPTION OF PRE-COPULATORY BEHAVIORS

Announcement Display.—After introduction to the aquarium of an adult female or after contacting her dragline on land or water, the male begins the first phase of signaling. This involves “leg-waving” and “jerks.” The former includes lifting legs I, usually in irregular alternation, but sometimes synchronously, with these legs typically being held extended straight or just slightly arched (Fig. 1). Most often, the tarsus describes a vertically elliptical path. On land the male walks with slow, erratic movements

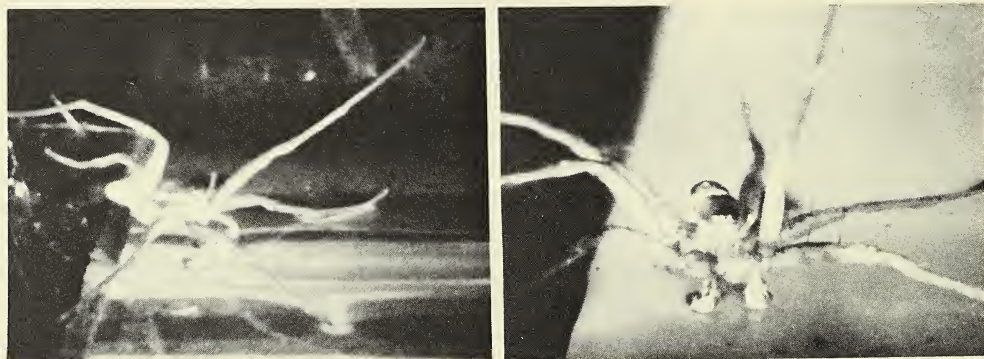


Fig. 1.—Lateral and front views of a male *Dolomedes triton* performing leg-waving (leg I stiffly elevated) while entering the water from the female's resting site and while moving on the water, respectively. (Photographs of frames of Super 8 mm movie film exposed at 18 frames/sec.)

and places his own dragline as he advances. On water his body is close to the surface, his legs almost horizontally extended, and his palps rest on the surface in a tightly flexed position. When the presumed chemical stimulus is strong, the very high lifting of legs I gives way to rapid, simultaneous tapping movements, especially on land.

At irregular intervals, while holding all the legs in contact with the substrate, the male performs one to three “jerks.” Each results from one or, more typically, two partial flexions and extensions at the femoro-patellar joint of legs I and, to a much less degree, legs II. A noticeable effect of the jerk on water is a single or double burst of concentric surface waves spreading outward from the male. Each burst results from a downward thrust of the anterior legs as they jerk in the above-described movement. When the spider is on land, the jerk is a much less obvious behavior due to the absence of the easily seen surface waves that attract our attention when the spider is on water.

Courtship Behavior.—As mentioned above, behaviors that presumably provide two long-distance signals—leg-waving (probably visual) and jerks (probably vibratory)—give way to close-range signaling when the female pheromone is in high concentration. This occurs when the male contacts the resting site, the female herself, or, in some cases, the silk draglines of the female. He then begins to perform rapid simultaneous tapping of legs I, both legs being lifted a relatively short distance above the substrate, with quivering of the distal segments. The male continues to lay down his own dragline.

In response to the male’s approach, the female may briefly “drum” on the substrate, including the water surface, by rapidly vibrating her palps; on water, surface waves result from this behavior. She then performs a behavior that is like a slow and exaggerated version of the male’s earlier leg-waving. Her legs I and/or II are waved in broad, circular paths while held rather stiffly extended. Leg interplay results from the male’s leg-tapping and the female’s leg-waving, such an interaction having been noted in *D. scriptus* for one-half hour prior to copulation (Carico 1973).

RESPONSES OF MALES TO VARIOUS WATERS

1. Aquarium of Male.—Method: We used 15 males in a series of 20 tests for responsiveness to aquaria that had housed five other males. In 10 trials, test males had been housed in aquaria of their own; in the other 10, test males had been housed in plastic cages with paper floors.

Results: None of the males showed jerks, leg-waving, or agonistic display within 10 min after introduction to the water surface.

2. Aquarium of Intact Female.—Method: Ten males were used in 20 tests for responsiveness to aquaria that had housed nine intact females.

Results: Leg-waving and jerks occurred within the 10-min test time in 16 of the 20 tests. In 14 of the 16 cases this behavior began on the water surface, prior to contact with the female’s wooden resting site.

3. Aquarium of Female with Sealed Spinnerets.—Method: We used 11 males in 20 tests for responsiveness to aquaria that had housed one of three females whose spinnerets had been sealed with paraffin at least two days prior to testing.

Results: Leg-waving and jerks occurred within the 10-min test time in 10 of the 20 tests.

4. Water Contacting Silkless Female for One Hour.—Method: We wished to determine if males would respond to water that had contacted the female’s integument for a relatively short time, as well as to minimize the possibility that responses in aquaria resulted

from an airborne component that accumulated above the water surface. We used five females with sealed spinnerets in a total of 20 tests. For each test, a female was placed into a covered plastic vial containing 50 cc of distilled water. The vial was turned over at 5-min intervals to insure adequate contact of the female with the water. After 1 hr the female was removed and the water poured into a shallow bowl (19 cm in diameter). The test male (nine were used) was placed on the water surface and observed for 10 min.

Results: Leg-waving and jerks occurred in five of the 20 tests.

5. Aquarium of Intact Female Restricted by Screening.—Method: We wished to prevent the female from wandering more than about 10 cm beyond her wooden resting site, so that, unlike Exper. 2, the male could not directly encounter water through which the female might have swum, or on which she might have walked. We mounted a piece of plastic window screening obliquely from the top to the bottom of each of two aquaria (Fig. 2). Any pheromone produced by the female would have to disperse from the release area near the resting site. The flaw in this design arose from the tendency of females to hang from the screen—well above the water—rather than use the resting site. We urged them down to the water-level resting site each day, so that at least part of each day included contact with the water.

We used 10 males in a total of 20 tests for responsiveness to the aquaria of 3 intact females. For each test the female was removed and a glass barrier placed in the middle of the aquarium. Thus, during the initial phase the male could neither touch any surface that the female had directly touched (the screen included) nor any of her draglines. After spending 10 min on the water beyond the glass barrier (“A” of Fig. 2), he was transferred to the female’s living area (“B”). If he did not court in the latter area within 10 min, we assumed him to be sexually unresponsive and did not include his behavior in the 20 tests. Thus, all the males included in the scoring for this experiment were ones that at the least responded to the presumably adequate concentration of pheromone in area B.

Results: Leg-waving and jerks were shown by males in area A in five of the 20 tests. (Results of Experiments 1-5 are summarized in Table 1.)

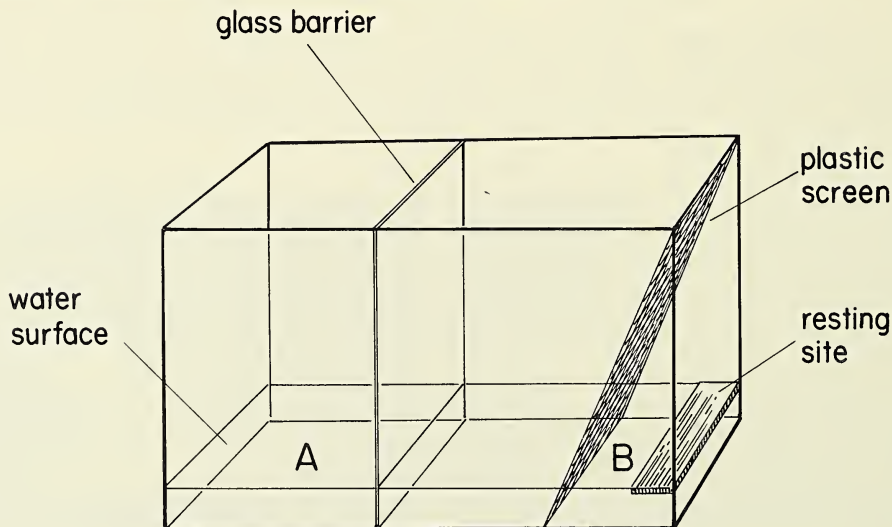


Fig. 2.—Setup for Experiment 5. A female *Dolomedes triton* is restricted to area B of the aquarium for several days by a plastic screen. She is removed, a glass barrier is inserted, and a male is introduced to the water surface in area A. After 10 minutes he is transferred to area B.

RESPONSES OF MALES TO VARIOUS DRAGLINES

a. Conspecific Adult Female Dragline (Dry Substrate).—Method: We combined two methods developed by previous workers to obtain single draglines from spiders. The substrates were those used by Tietjen (1977): glass plates (41 X 5 cm) to which three glass rods had been glued transversely at 10-cm intervals. This insured that most of the line would be elevated about 0.5 cm (the rods' diameter) above the plate, enabling males to follow while walking. We used Work's (1981) method to force the spider to place the line lengthwise along the plate (and over the rods). The spider was put beneath an inverted beaker at the "start" area at one end of the plate. After the spider fixed an attachment disk to that site, we guided it slowly along the plate beneath the slightly raised beaker. At the other end of the plate, about 30 cm away, we waited until a second disk was attached, urged the spider off the plate, and used masking tape to secure this next short section of dragline to the plate. Seven males were used to test the lines of four females in a total of 10 tests.

Results: After introduction to the start area, the male typically encountered the female's dragline during chemoexploration of the glass surface, the palps brushing against the substrate, as is well-known in lycosids and other wanderers. Leg-waving, leg-tapping, or jerks sometimes began even before the dragline itself was contacted, suggesting that pheromone was deposited on the glass during the female's brief rest at that site. After encountering the line, the male straddled it and advanced along its length, using his palpal tarsi (medial surface) and legs I to touch the line. Palpal stroking of the line thus was like that described for *Lycosa* spp. by Tietjen and Rovner (1980). Tapping or grasping the line with the claws of either leg I occurred at variable intervals. Following occurred in nine of the 10 tests.

b. Conspecific Male Dragline (Dry Substrate).—Method: Thirteen males were used to test the lines of seven adult male conspecifics in a total of 20 tests.

Results: In six of 20 tests, the dragline was followed a short distance ($< 1/3$ of the line); however, neither leg-waving nor jerks occurred.

c. Conspecific Subadult Female Dragline (Dry Substrate).—Method: Fourteen males were used to test the lines of two subadult female conspecifics in 20 tests.

Table 1.—Summary of experiments on *Dolomedes triton*. (Except for d, all experiments involve conspecifics; unless stated otherwise, all involve adults).

Stimulus situation	Tests yielding display	Total no. of tests	Tests yielding following	Length of line followed
1. Aquarium of male	0	20	—	—
2. Aquarium of female	16	20	—	—
3. Aquarium of silkless female	10	20	—	—
4. Water contacting silkless female	5	20	—	—
5. Aquarium of restricted female	5	20	—	—
a. Dragline of female	9	10	9	entire
b. Dragline of male	0	20	6	$< 1/3$
c. Dragline of subadult female	0	20	6	$< 1/3$
d. Dragline of heterospecific female	0	20	5	$< 1/3$
e. Dragline of female on water	9	10	9	entire

Results: As in (b), six cases of partial following without sexual responses occurred in the 20 tests.

d. Heterospecific Adult Female Dragline (Dry Substrate).—Method: Eleven males were used to test the lines of four adult female *Lycosa rabida* in 20 tests.

Results: Five cases of partial following without sexual responses occurred in the 20 tests.

e. Conspecific Adult Female Dragline On or Just Below Water Surface.—Method: After obtaining the draglines, we put the glass plates into empty 10-gal aquaria. Then we poured distilled water slowly onto the aquarium floor until the level reached the top of the glass rods, i.e., until the water surface was just below, equal to, or slightly above the dragline, depending on the section of the line. One of five males then was introduced to the water in the start area.

Results: Following of the entire line, accompanied by leg-waving and jerks, occurred in nine of the 10 tests. In following, the male rowed along, with legs II and III providing the propulsion. The palpal tarsi rested on the water, strongly flexed, and were not used to stroke the line. The fourth legs dragged behind, while legs I were used to locate and pull on the line: After swinging broadly across the surface, the right or left leg I eventually located the line and grasped it with the claws. The spider then used this leg to pull forward, this being the second method of advancing along the line (Fig. 3). (Results of Experiments a-e are summarized in Table I.)

DISCUSSION

Kaston (1936) had demonstrated the existence of a courtship-eliciting, ether-soluble substance on the integument of female *Dolomedes scriptus*. He also showed that a sex pheromone was bound to the female's silk but was not released onto the substrate simply by contact of the integument with the cage floor. Our primary purpose was to examine the nature of such chemical signaling on a watery substrate, a more natural situation for such aquatic species as *D. scriptus* and *D. triton*. We also wished to find out if male pisaurid spiders follow draglines and if courtship in another member of the genus *Dolomedes* resembled that described by Kaston (1936) for *D. scriptus*.

In response to the presence of a presumed female sex pheromone, male *D. triton* show leg-waving and jerks, the latter being a distinctive indicator of sexual excitement in males on water due to the production of concentric surface waves. When the pheromone concentration is high, especially on contact with the female or her resting site, the announcement display of leg-waving and jerks gives way to rapid leg-tapping. If the female waves her legs I and II in response, prolonged bouts of leg interplay between the partners result. Thus, pre-copulatory behavior is triggered chemically and then includes vibratory and tactile signals. Leg-waving may also yield visual signals. While pre-copulatory behavior shares some elements with that of *D. scriptus* (Kaston 1936), *D. triton*'s jerk is an important addition. We anticipate that future experiments will reveal a communicatory function for the surface waves produced by the male's jerk (and perhaps for the female's palpal "drumming", which also produces concentric surface waves). The resemblance to the surface wave signals of water striders (Hemiptera, Gerridae), well-studied by Wilcox (1972, 1979), is suggestive of such a function.

Contact with the water of a female's aquarium usually triggers pre-copulatory behavior in males (Exper. 2), whereas a male's aquarium does not (Exper. 1). Silk from the female

need not be present on or in the water to yield a medium level of responsiveness in males (Exper. 3); however, the level of positive responses is higher when the female has been in contact with the water for days rather than only for 1 hr (Exper. 4). The occurrence of some responses to the water poured into the bowl from the vial (Exper. 4) indicates that the responsiveness of males in the previous experiments did not depend on an airborne component that built up over the water in the aquarium, although such a factor could contribute to the total effect. One would not expect olfaction to be important in *D. triton* on the basis of Kaston's (1936) having found no role for it in *D. scriptus*.

Based on the above experiments, as well as Exper. 5, we hypothesize that the pheromone secreted onto the female's integument also spreads out on the surface of the water, as would a non- or mildly polar compound—perhaps a lipid or steroid. Sarinana et al. (1971) had postulated that the sex pheromone on the lycosid spider *Pardosa ramulosa* was a lipid, based on solubility characteristics, supporting the earlier view of Kaston (1936) on this subject.

Since female *D. triton* remain at the same site for days and remain motionless at one spot on the water for up to at least 2 hr (J. Sefton and Rovner, unpubl.), it seems possible to have a build-up of pheromone on the water surrounding the female. Thus, male *D. triton* could detect the female before touching her dragline or making visual or direct contact with her. The male's signals in response, likewise effective day or night, probably inhibit the female's predatory behavior. Indeed, several instances of cannibalism did occur when males failed to respond to the water of aquaria containing what we assumed were food-sated females during later pairings undertaken to study male-female interactions.

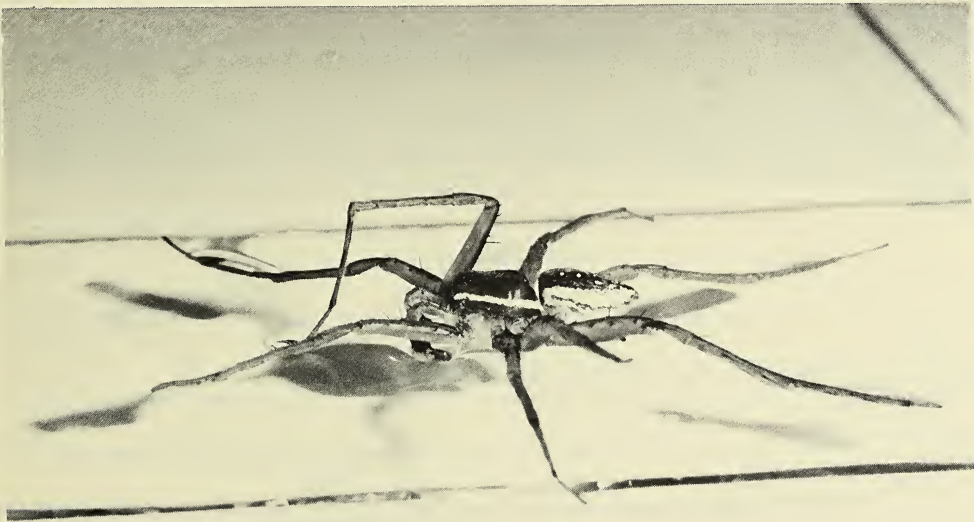


Fig. 3.—Dragline-following on water by a male *Dolomedes triton*. The spider is advancing along the silk thread (not visible) by grasping it with the claws of one foreleg and pulling himself forward; the arched right foreleg has just completed such a pull. Rowing movements of legs II and III also aid forward progression.

Male *D. triton* may partially follow the draglines of conspecific males (Exper. b) and subadult females (Exper. c), as well as heterospecific females (Exper. d); however, they do not show sexual responses. The tendency to respond to silk, irrespective of a chemical that may be present or absent on it, has most recently been seen in studies using T-mazes that involved agelenids (Roland in ms.). Apparently, lacking the adequate chemical stimulus of the female pheromone, the "incorrect" threads still provide sufficient mechanical and possibly some general chemical stimuli to elicit low levels of following behavior in some males. The distinction between chemical and mechanical cues in dragline-following by lycosids was well-demonstrated by Tietjen (1977), who found that imitation lines—even human hairs—would be followed for some distance by males that were already in a following mode from chemical stimulation.

On both dry substrates (Exper. a) and water (Exper. e), male *D. triton* readily follow adult female's draglines. Thus, the pheromone bound to the silk of these aquatic spiders must be unlike those used by various lycosids, which are degraded by water (Dondale and Hegdekar 1973, Hegdekar and Dondale 1969, Tietjen 1977). Instead it may turn out to be a mildly polar compound, as has been suggested for the silk-bound female pheromone of the salticid *Phidippus audax* (N. Oden, pers. comm.) or a non-polar compound. Of course, whether the dragline of *D. triton* retains its potency on water as long as it does on land remains to be determined. Nevertheless, the ability of males to advance along the line by rowing and pulling enables them to locate the female when the male is approaching via the water surface. Thus, a long-distance, orientational role for chemical signaling on water can be added to the close-range, courtship-eliciting aspects that were examined in Kaston's (1936) pioneering work on *D. scriptus* and other wandering spiders.

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FORAGING PATTERNS AND TIME BUDGETS OF THE CRAB SPIDERS *XYSTICUS EMERTONI* KEYSERLING AND *MISUMENA VATIA* (CLERCK) (ARANEAE: THOMISIDAE) ON FLOWERS

Douglass H. Morse

Division of Biology and Medicine
Brown University
Providence, Rhode Island 02912, USA

ABSTRACT

Xysticus emertoni Keyserling (Araneae: Thomisidae) hunted regularly for insects on flowers of common milkweed (*Asclepias syriaca* L.), but only infrequently on goldenrod (*Solidago juncea* Ait.) and rarely on pasture rose (*Rosa carolina* L.) Individuals usually remained less than two days on a milkweed stem and fed primarily on honey bees (*Apis mellifera* L.) and nocturnal noctuid and geometrid moths. The largest common prey, bumble bees (*Bombus* spp.) were very seldom captured. *Misumena vatia* (Clerck), a second species of thomisid that hunted on flowers in the study area, by contrast hunted frequently on milkweed, goldenrod, and pasture rose. Individuals remained over twice as long on milkweeds and captured bumble bees regularly, as well as honey bees and nocturnal moths. As a consequence, they captured over twice as much prey biomass per day as *Xysticus*. I hypothesize that the difference between the two species in time spent per stem and in frequency of using goldenrod and pasture rose is a consequence of the difference in success of prey capture, primarily a failure of *Xysticus* to include bumble bees regularly in their diet. *Xysticus emertoni*, a member of a largely litter-inhabiting genus, probably secures the majority of its food there, rather than at flowers.

INTRODUCTION

Xysticus emertoni Keyserling (Araneae: Thomisidae) is one of two crab spiders that regularly forage on milkweed (*Asclepias syriaca* L.) growing along the coast of Maine. *Xysticus* is an ambush hunter that lies in wait for the large numbers of insects that are attracted to milkweed when its flowers are producing nectar.

Xysticus emertoni is a medium-brown spider, with dark brown markings on its abdomen. It may range up to 12 mm in length (cephalothorax + abdomen) and immediately prior to egg-laying, females may weigh as much as 250 mg. Their robust cephalothorax and legs are relatively larger than those of the other common crab spider found on milkweed in the study area, *Misumena vatia* (Clerck), but their abdomen is relatively smaller. *Xysticus emertoni* is a member of a primarily litter-dwelling genus, which may account for these differences, although a few species of *Xysticus* do hunt regularly in flowers (Gertsch 1939, 1979).

Earlier (Morse 1981a) I reported on the foraging patterns and time budget of *M. vatia* on milkweed and other flowers in the study area. Since *Xysticus* is a member of a more

cursorial ground and litter-dwelling group of crab spiders than *Misumena* (Gertsch 1939, 1979), it seemed appropriate to compare its foraging on flowers with that of *Misumena*, which appears to hunt almost exclusively at flowers, at least when in its last instars. Given the somewhat different attributes but similar size of these two species, a comparison between them may provide useful insight into the factors that dictate the foraging patterns of crab spiders, as well as ambush predators in general.

In particular, I relate differences in their behavior on milkweed flowers to differences in hunting success. Hunting success has important implications for both giving-up times (Charnov 1976) of individuals on a given milkweed inflorescence or stem and the frequency with which they occupy other common flowers.

METHODS

This study was conducted in Bremen, Lincoln Co., Maine during July and August of 1979, 1980, and 1981. The spiders, all adults, occupied a field and some adjacent low brushy growth that supported clones of milkweed. Twenty of these individuals were marked with pens using indelible ink.

Asclepias syriaca grows from rhizomes in clones of one to several thousand stems (Woodson 1954). The clones in which these spiders were studied contained 200-400 flowering stems. The flowering stems in the study area produced 1-5 inflorescences (umbels), each with 20 to 70 flowers. When in the peak of bloom milkweed attracts large

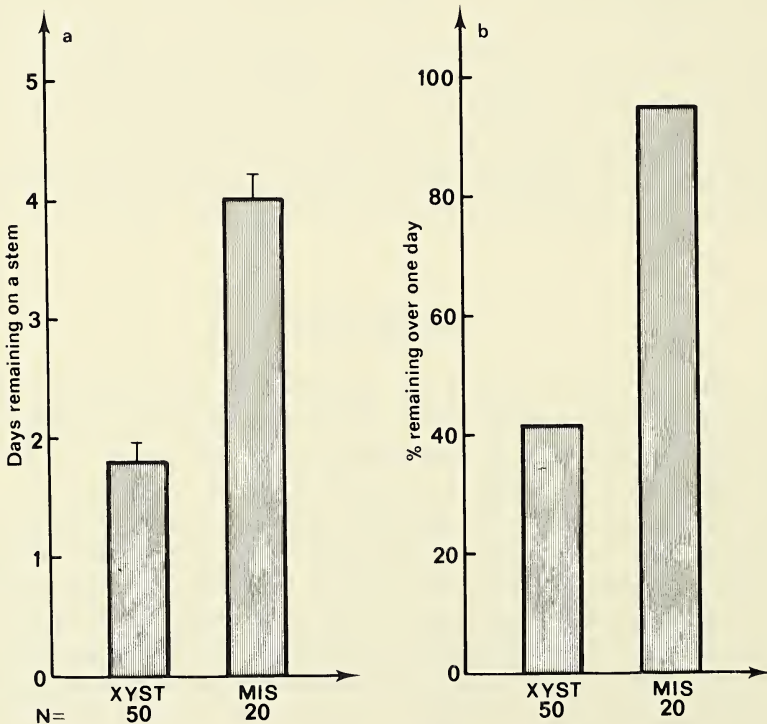


Fig. 1a.—Number of days that *Xysticus* and *Misumena* remained on a stem, ± 2 S. D. ($p < 0.001$ in a two-tailed Mann-Whitney U Test). Fig. 1b. Percentages of *Xysticus* and *Misumena* remaining on a stem for more than one day ($X^2 = 14.29$, $p < 0.001$, $df = 1$, using original data).

Table 1.—Numbers of prey captured, with percentage of total biomass in parentheses.

Food item	<i>Xysticus</i>	<i>Misumena</i>
Moths (Noctuidae, Geometridae)	14 (32.8%)	21 (23.3%)
<i>Apis mellifera</i>	7 (21.4%)	25 (34.1%)
Other Hymenoptera (excluding <i>Bombus</i>)	6 (13.8%)	3 (4.1%)
Jumping spider (Salticidae)	1 (8.1%)	
Tachinid flies (Tachinidae)	10 (13.8%)	5 (3.1%)
Ladybird beetles (Coccinellidae)	5 (8.1%)	
Other	1 (2.1%)	7 (2.1%)
<i>Bombus</i> spp.		10 (33.3%)

numbers of insects, especially large social bees (Apidae) and nocturnal moths (primarily Noctuidae and Geometridae) in the study area (Morse 1982). Umbels bloom sequentially up a stem, and the different stems are not in perfect synchrony, so that large numbers of flowers are in nectar-producing condition at a clone for two weeks or more each year.

Spiders were monitored hourly between 0730 and 1730, the period during which they captured virtually all of their diurnal prey. In that *Xysticus* almost always retained their food items for over an hour (similarly to *Misumena*), it was possible to obtain an accurate estimate of the amount and type of foods taken. Limited nighttime observations were also made, and corpses of prey still being consumed or located below the spiders early the following morning were recorded. Total biomass captured was obtained by using the mean live weights of specimens of the various prey species (Morse 1979, 1981a).

Several spiders (8) were also monitored continuously for one day or more, permitting me to quantify the numbers of potential prey and attacks made on them during they day. This permitted calculation of foraging success and response to different prey species.

In the following sections I will first present the results of this study on *Xysticus* and then compare them with *Misumena*'s performance on milkweed. Unless otherwise indicated, the data on *Misumena* come from a companion study (Morse 1981a) that compared the foraging patterns and time budgets of that species on three different species of flowers that they regularly occupied.

RESULTS

Time spent on a stem.—*Xysticus* averaged less than two days on a stem (Fig. 1a), with a maximum of four days. Less than half of the individuals remained more than one day (Fig. 1b). In contrast, *Misumena* remained an average of four days on a stem (Fig. 1a), and virtually all individuals remained for more than a day (Fig. 1b). Both of these between-species differences were significant (Fig. 1). Since individual stems (or even umbels) usually attracted substantial numbers of insects for several days, changes in prey abundance were unlikely to account for any of these differences.

Prey captured.—Nocturnal moths and honey bees (*Apis mellifera* L.) made up the largest proportions of biomass taken by the *Xysticus* monitored (Table 1). Other frequently-captured prey included certain hymenopterans and tachinid flies (Tachinidae). *Xysticus* also captured several ladybird beetles (Coccinellidae), generally regarded as toxic (Wickler 1968). Perhaps *Xysticus* is not sensitive to toxic factors, since one individual was

observed feeding on a last-instar monarch butterfly (*Danaus plexippus* L.) larva (not included in the spiders censused for food captures). Additionally, one *Xysticus* captured a female jumping spider (*Phidippus* sp., Salticidae) larger than itself. Surprisingly, although bumble bees were the commonest visitors to the clones of milkweed upon which these observations were made (Morse 1981b; Morse and Fritz in press), none were captured in this sample.

Bumble bees and honey bees were the most important prey items of *Misumena*, with nocturnal moths also playing an important role. Thus, a major difference was the absence of bumble bees from *Xysticus*' prey items, but relatively higher proportions of other items, such as tachinid flies, solitary bees, and ladybird beetles (*Xysticus* have very occasionally been found feeding on bumble bees at other times, so this difference is not really absolute). Allocation of biomass from the various prey types (Table 1) differed highly significantly between *Xysticus* and *Misumena* ($X^2 = 20.52$, $p < 0.001$, $df = 5$, using all categories but the jumping spider and ladybird beetles). Although one might initially attribute this marked difference to niche partitioning, the densities of both spiders were so low [maximum count of 14 *Xysticus* ($\bar{x} = 9.5 \pm 3.6$ S.D. during 18-25 July) and 7 *Misumena* ($\bar{x} = 5.0 \pm 1.5$ D.S. during 18-25 July) on 387 flowering stems] that it is very unlikely that this factor played any role in the differences noted.

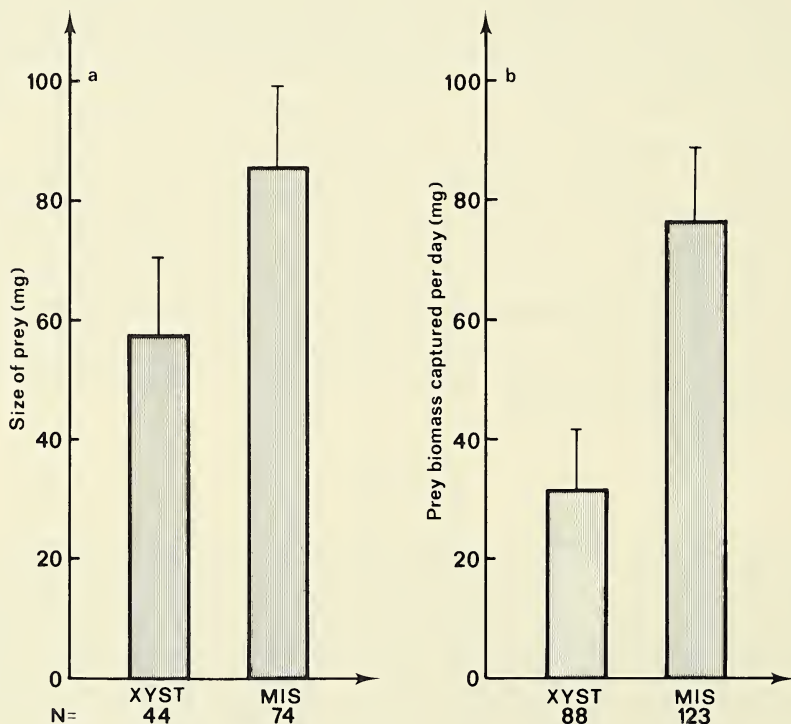


Fig. 2a.—Size of prey captured by *Xysticus* and *Misumena*, ± 2 S. D. ($U = 591$, $p < 0.002$ in a one-tailed Mann-Whitney U Test). Fig. 2b. Biomass of prey captured daily by *Xysticus* and *Misumena*, ± 2 S. D. Average rates of capture of *Xysticus* were significantly lower than those of *Misumena* ($U = 96$, $p < 0.025$ in a one-tailed Mann-Whitney U Test). Additionally, *Xysticus* observed only one day captured an average of 19.2 mg of prey/day ($N = 15$); *Misumena* observed only one day, 37.5 mg/day ($N = 2$).

Table 2.—Number of prey within attack range (within one spider body-length), prey attacked, and capture success of *Xysticus* and *Misumena*. Observations made during constant monitoring of *Xysticus* (84.25 hr) and *Misumena* (107.50 hr) throughout the day. The total number of observations is in parentheses.

Prey	<i>Xysticus</i>			<i>Misumena</i>		
	Prey within range	Prey attacked	Prey captured	Prey within range	Prey attacked	Prey captured
<i>Bombus</i>	0.78 (66)	0.18 (15)	— (0)	0.80 (86)	0.26 (28)	0.02 (2)
Diptera	0.05 (4)	0.05 (4)	0.02 (2)	0.02 (2)	0.02 (2)	0.02 (2)
<i>Apis</i>	0.10 (8)	— (0)	— (0)	0.30 (32)	0.14 (15)	0.01 (1)
Other	0.07 (6)	0.05	0.04 (3)	0.03 (3)	0.01 (1)	— (0)

Xysticus' prey were significantly smaller than those of *Misumena* (Fig. 2a). This difference occurred largely because *Xysticus* failed to capture bumble bees, the largest common prey at these flowers.

Rate of capture of biomass.—*Xysticus* captured an average of 23.1 mg of diurnal prey per day and additional 8.5 mg of nocturnal moths, for a total of 31.6 mg of prey per day. *Misumena*, on the other hand, captured, over 2.5 times as much diurnal prey and over twice as much nocturnal prey biomass. The overall difference is significant (Fig. 2b).

Daily time budget.—*Xysticus* spent about 85% of their time hunting on the plants and 15% of the time feeding (Fig. 3). The greatest proportions of the hunting time were spent under the umbels and the flowers of the umbels. The times allotted to hunting and feeding were nearly identical to those of *Misumena* (Fig. 3); however, the locations of the hunting sites were markedly and significantly different (Fig. 3). Most of *Misumena*'s hunting was done on top of the inflorescences, rather than under or in the inflorescences, as with *Xysticus*.

Attacks on prey and success of capture.—The frequency of attacks and success of capture were determined from studies on continually-observed individuals (Table 2). Bumble bees were the most frequent visitors, and the most frequent species to come within strike range (defined as one spider body-length). Only about one-fourth of these bumble bees were attacked, and none were captured. Numbers of other visitors during the observation period were too small to make detailed comparisons, but they tended to be attacked with considerably higher frequency than the bumble bees. However, *Xysticus* attacked nearly as high a proportion of bumble bees that came within range as did *Misumena* (25.8% vs. 32.6%). This difference is not significant ($\chi^2 = 0.53$, $p > 0.3$, $df = 1$, using data in Table 2). The data suggest a possible trend for *Misumena* to respond to honey bees more frequently than do *Xysticus*, but the frequency of honey bees available to *Xysticus* was too low to permit testing.

Use of other flowers by *Xysticus*.—No observations were made of marked *Xysticus* individuals moving between milkweed and other species of flowers, although *Xysticus* were occasionally seen on other species of flowers, including cow vetch (*Vicia cracca* L.) growing within a few meters of the milkweed. Given the frequency with which they moved on and off milkweeds, one would expect them to shift between plant species where it would be profitable. However, of the other flowers attracting the most potential prey (and *Misumena*), *Xysticus* was seen only twice on pasture rose (*Rosa carolina* L.) over several summers of intensive observations of *Misumena*. Although observed more

frequently on goldenrod (*Solidago juncea* Ait.), it was not seen often enough there to obtain data for quantitative analysis. A *Xysticus* observed on goldenrod did, however, capture a bumble bee.

DISCUSSION

Characteristics of *Xysticus*.—*Xysticus*' visitation patterns on milkweed differed markedly from those of *Misumena*. Individuals remained at a site for a much shorter period of time, and once marked individuals disappeared they were only seldom resighted, as opposed to *Misumena*, in which individuals leaving a foraging site were frequently rediscovered when stems were carefully searched. This suggests that adult *Xysticus* spend much of their time in the litter, as opposed to adult *Misumena*, which spend virtually all of their time on flowering plants, and most of that on the flowers, or at least in searching for flowers. This difference is perhaps not surprising, in that *Xysticus* is a member of a large genus composed primarily of litter-dwelling species (Gertsch 1939). The dull brown coloration of *Xysticus* is similar to that of many litter-dwelling spiders, and its larger legs probably contribute to making it more cursorial than *Misumena*.

Suitability of different flower species as hunting sites.—There is, however, another aspect to *Xysticus*' brief appearances on these flowers. Their rate of prey uptake on milkweed was markedly lower than that of *Misumena*, and it is thus possible that these sites are simply not highly profitable ones for them. *Xysticus* were almost completely

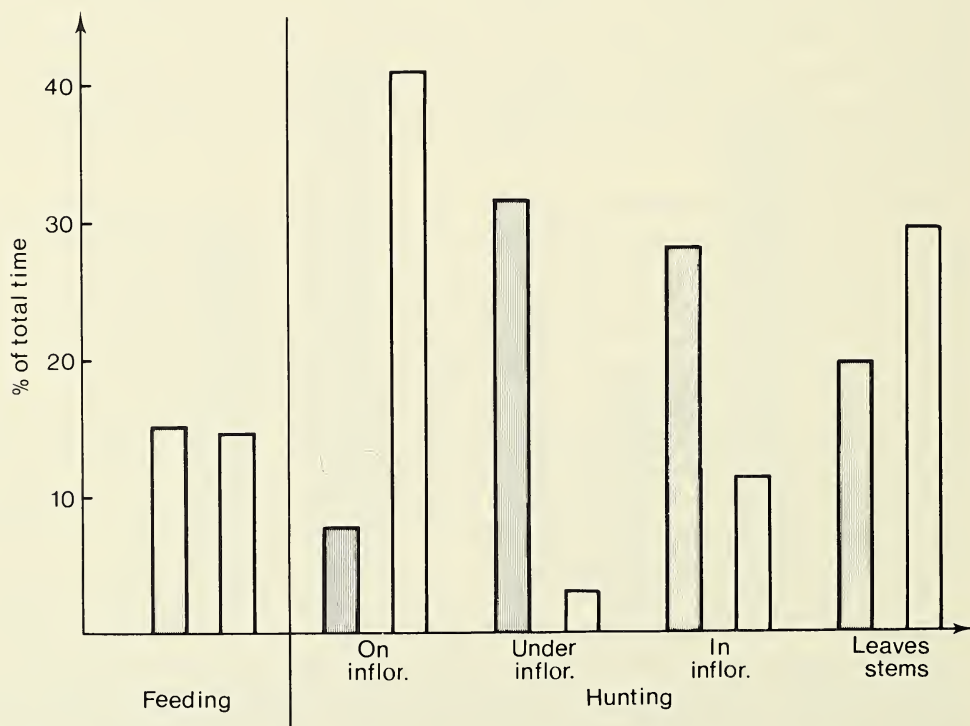


Fig. 3.—Diurnal time budget of *Xysticus* (black bars) (544.5 hr) and *Misumena* (white bars) (716.0 hr) on milkweed. The hunting positions of the two species differed significantly from each other ($X^2 = 29.23$, $p < 0.001$, $df = 3$, using an arcsine transformation).

unsuccessful in capturing bumble bees, although these bees were the commonest visitors to the flowers, and constituted one of the two most important items (over 40%) in the food of *Misumena* on milkweed (the other being honey bees). Failure to incorporate these prey into their diet may make the difference between milkweed inflorescences being a profitable or unprofitable hunting site for *Xysticus*. Further, milkweed was a more profitable hunting site for *Misumena* than either goldenrod or pasture rose (Morse 1981a), suggesting that it may provide the richest source of food for ambush hunters. It was also the only one of the three flower species at which bumble bees were not the overwhelmingly most important prey item for *Misumena*. *Misumena* captured nearly twice as much biomass per day on goldenrod as on pasture rose, and further, its diet was more varied there than on pasture rose, where virtually the entire biomass was composed of bumble bees. Thus, there was progressively less available food, and markedly fewer prey other than bumble bees, on goldenrod and pasture rose than on milkweed. These two factors are consistent with the only occasional appearance of *Xysticus* on goldenrod, and its virtual absence from pasture rose.

The difference in hunting behavior of *Xysticus* and *Misumena* in the milkweed inflorescences could in part account for the differences in prey capture patterns. *Xysticus* remained more concealed than did *Misumena*, which could either be a consequence of its hunting patterns in the litter, or be associated with concealment from prey or predators. *Xysticus* should be more conspicuous against the white background of milkweed inflorescences than *Misumena*, which is typically white on milkweed and cryptic both at visual and ultraviolet wave lengths (Morse, unpubl.). In spite of this, the proportion of approaching bumble bees attacked by *Xysticus* was not significantly lower than that of *Misumena*.

Giving-up times.—The short times (= giving-up times of Charnov 1976) spent on milkweed by *Xysticus* are probably best explained in the context of environmental patchiness, given this spider's presence both on milkweed stems and in the litter layer. Assuming that *Xysticus* have energetic demands comparable to those of similar-sized *Misumena*, their relatively low success and short giving-up times on milkweed stems suggest that their rates of prey capture often fall below those to be obtained at hunting sites away from the flowers (see Charnov 1976; Pike, Pulliam and Charnov 1977). In fact, these *Xysticus* exhibited giving-up times that were similar to those of *Misumena* on senescent milkweed stems (Morse and Fritz, 1982), suggesting that the two species responded to very different densities of prey. Morse and Fritz (1982) found that numbers of insect visitors, rather than more direct measures (e.g., attack or capture frequency), provided the best correlation between observed and predicted frequencies of umbel occupation by *Misumena*. However, since umbels occupied by *Xysticus* were visited by insects at frequencies similar to those occupied by *Misumena*, actual capture rates may play an important direct role in *Xysticus*' choice of umbels. If the two species responded in different ways to these various cues, this would be of major interest in untangling the web of variables that dictate the choice and continued occupation of a hunting site. One could experimentally test whether frequency of visitation to an umbel does play an important role in determining *Xysticus*' giving-up time by increasing the frequency of prey visitation, probably in a screened flight cage. The predicted frequency of insect visits necessary to extend *Xysticus*' giving-up time to that of *Misumena* can be determined by calculating the number of insect visits necessary for *Xysticus* to realize a hunting success comparable to that of *Misumena*. Fig. 2b suggests that an increase in visitation frequency of over two-fold would be required.

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RESEARCH NOTES

ON THE ALLEGED ABSENCE OF FERTILIZATION
DUCTS IN THE GENUS *POLENECIA*
(ARANEAE, ULOBORIDAE)

When I received the recent paper by Opell (1979, Bull. Mus. Comp. Zool. Harvard, 148:443-549) on american Uloboridae, I was highly astonished by the discovery of the haplogyne nature of some genera. In a paper then still in press (Brignoli, P. M. 1979, Rev. Arachnol., 2:275-282) I had indeed considered a species of one of these genera, *Polenecia producta* (Simon, 1873) as typically entelegyne. Fearing to have misinterpreted the structure of the vulva of this species, I re-examined my material; the results can be seen in Figs. 1-5.

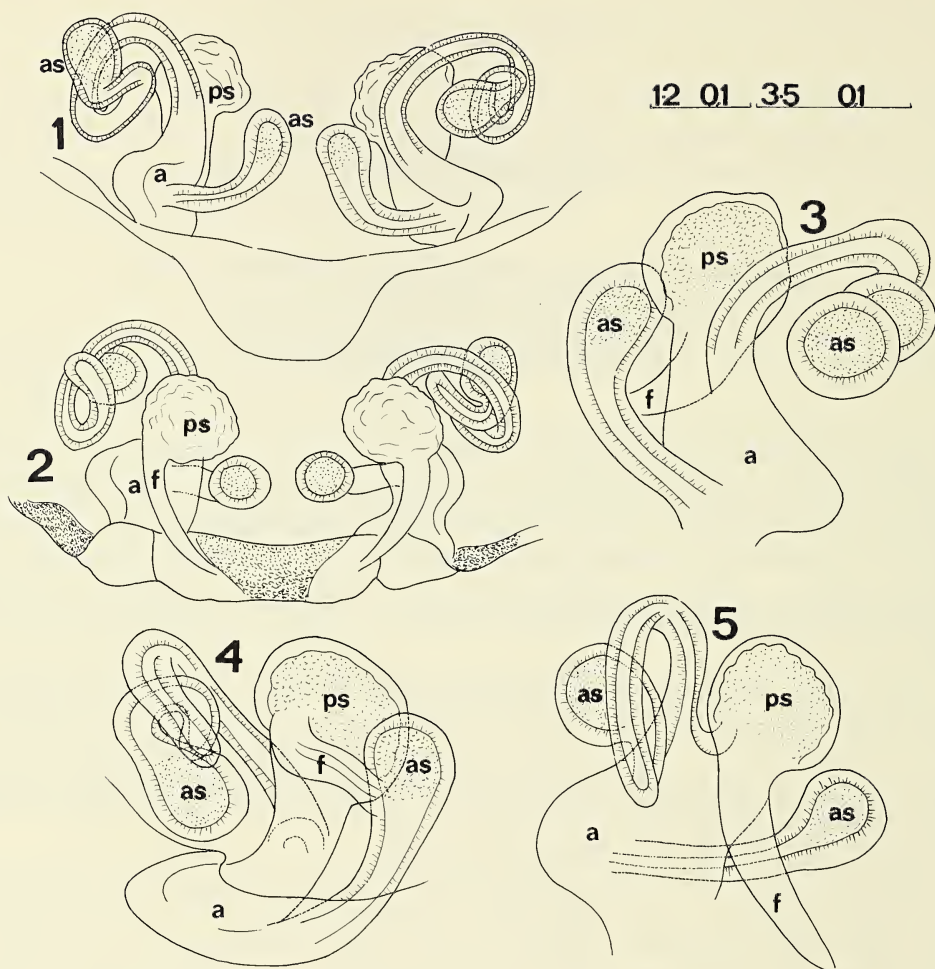
Each half of the vulva of *Polenecia producta* consists, I think, of an atrium (a), weakly sclerotized, which opens on the internal margin of the epigyne and from which depart three ducts of different lengths, leading respectively to a pair of accessory spermathecae (as 1, as 2) with long connecting ducts and to a principal spermatheca (ps), heavily sclerotized and internally relatively complicated, with a very short connecting duct. From this spermatheca departs a long fertilization duct (f).

Opell has interpreted the principal spermatheca as an "accessory gland." In addition to the evident connection to the atrium (Figs. 3-4) the heavy sclerotization of this structure also makes Opell's hypothesis unlikely, for it is a highly unusual feature for a "gland," which suggests an ectodermic origin. In no other spiders are "sclerotized glands" known; on the/contrary, sclerotized and internally complicated spermathecae are very common, for example in the Agelenidae.

As a whole, the vulva of *Polenecia* resembles strongly that of some Hahniidae; in many species of that family there is a weakly sclerotized atrium and there are two pairs of spermathecae, connected with the atrium by two separate ducts of different lengths, uniting in a single, less sclerotized, duct shortly beyond the atrial region (for illustrations, see Harm. M. 1966, Senckenberg. biol., 47:345-370 and Brignoli, P. M. 1978, Entom. Basiliensis, 3:31-56). The only relatively unusual feature in the vulva of *Polenecia* is in the marked structural difference between the two types of spermathecae.

My findings throw some doubts also on the interpretations by Opell of the vulvae of *Tangaroa*, *Waitkera*, *Ariston*, *Siratoba* and *Hyptiotes*. (I hope to find the time for examining this last genus in the near future). Opell considers the Uloboridae as an unique example of a family uniting together haplogyne and entelegyne genera. More research is necessary to ascertain if this is truly the case, but at the moment I am not inclined to accept Opell's hypothesis.

The presence of a fertilization duct is a physiologically important character, because it indicates that the process of fertilization is different from that in the true haplogynes. In



Figs. 1-5.—*Polenecia producta* (Simon, 1873): 1, vulva, ventral aspect; 2, vulva, dorsal aspect; 3-5, one half of the vulva magnified, ventrally, latero-dorsally and latero-ventrally (in this order); "as" accessory spermatheca, "a" atrium, "f" fertilization duct. Scales in mm.

the entelegynes the eggs are fertilized in the *uterus externus* (Wiehle, H. 1967, Senckenberg. biol., 48:183-196), which is evidently completely inside the body; in the haplogynes the eggs are fertilized more externally, in the atrium (or *bursa copulatrix*) which is not exactly homologous with the *uterus externus*. A certain confusion has arisen from the use of this term for both groups of spiders. The differences between the two kinds of *uterus externus* are well shown in figs. 8 and 29 of Wiehle (op. cit).

The details of the fertilization are still largely unknown, but the physiological distance between a haplogyne and an entelegyne spider is considerable, and, *mutatis mutandis*, is comparable with that between a placental and a non-placental mammal.

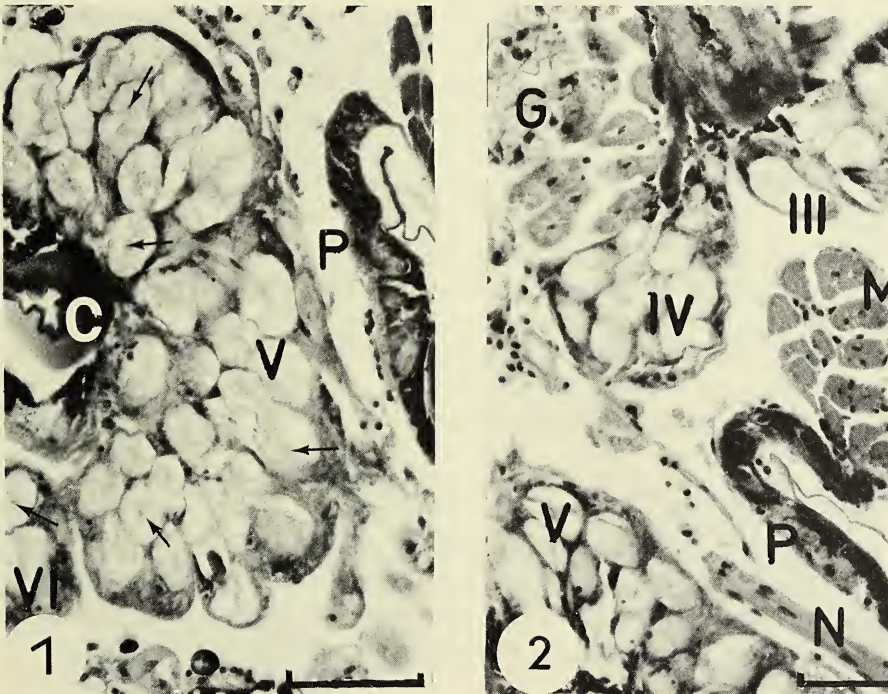
Paolo M. Brignoli, Istituto di Zoologia, Piazza Regina Margherita 7, 67100 L'Aquila, Italy.

COXAL GLANDS OF THE GENUS *METEPEIRA* (ARANEAE, ARANEIDAE)

As pointed out by Levi (Levi, H. W. 1977, Bull. Mus. Comp. Zool. Harvard, 148:185-238), the spiders of the american genus *Metepeira* are easily distinguished from other Araneidae by their light eye region, white median line on sternum, relative length of the leg segments, small male palpus, weakly sclerotized epigynum and the special composite web. However, there is a feature of internal anatomy that is distinctive, among Araneidae, to the genus *Metepeira*: the presence of conspicuous coxal glands.

I first discovered these organs on the occasion of a histological survey of specimens of *Metepeira incrassata* F. P.-Cambridge, a species from el Estado de Veracruz, Mexico (Lopez, A. 1978, C. R. Acad. Sc. Paris, 286: 407-409). In confirming the results of these previous histological investigations, I have recently observed them in specimens of three other species collected in the United States: *Metepeira labyrinthea* (Hentz) from Kentucky, *M. arizonica* Chamberlin and Ivie and *M. gosoga* Chamberlin and Ivie, from Arizona.

Each organ, when slightly magnified, appears as a cluster of vesicles with a sinuous endotheliform wall and fibrous contents. This honeycomb formation, bathed in hemolymph, lies against the cuticle and the hypodermal epithelium (Figs. 1, 2). In fact, the vesicles are large, curved basophilic cells having eccentric rounded nuclei; they enclose



Figs. 1, 2.—*Metepeira incrassata*, horizontal sections of the cephalic region. 1, Female. Coxal glands: pair V and a part of pair VI, the labyrinth of which is not visible; 2, Male. Pairs III, IV and V of coxal glands. Abbreviations: C = cuticle; G = gnathocoxal glands; M = muscles; N = palpal nerve; P = pharyngeal organ. Arrows = ductuli. Scale lines = 60 μ m.

extracellular cavities, 50 μm large on an average, containing fibrils which are probably nothing more than microvilli and, possibly, a secretion. A short ductulus originates in each cavity center (Fig. 1); it pierces the nearby integument which, apparently, is almost reduced to endocuticle and here forms a pitlike recess.

The organs in both sexes show an even, symmetrical distribution that horizontal sections clearly bring to light (Fig. 2). The last pair of glands (VI) is located behind the coxae of the first walking legs. Each of them is associated with a small dorsal labyrinth, 300 μm long, which shows the well-known basal striation in its acidophilic epithelium. The five other pairs are visible in a more anterior position that can be termed cephalic. Two of the pairs (pairs V and IV) occupy the bases of gnathocoxae: the external pair (V) is separated from the "pharyngeal organ" by the pedipalpal nerve, whereas the internal pair (IV) lies in front of the lateral fold of the pharynx, close to the maxillary glands (Fig. 2). Pair III is smaller, laterally located in the base of the rostrum, and lies adjacent and medially to pair IV (Fig. 2). Pair III is smaller, laterally located in the base of the rostrum, and lies adjacent and medially to pair IV (Fig. 2). Pair II is less conspicuous than the previous organs and lies beneath the cuticle of the rostro-cheliceral groove, exactly on a level with the paturon base. The forward pair (I) is extremely reduced and nestles under the integument of the ocular projection.

I regard all these organs as modified coxal glands, one "thoracic" (VI) and five others "cephalic", owing to their segmental arrangement, outlet locations, basic sacculus-like pattern and, chiefly, the close connection of pair VI with a recognizable, small, labyrinth. They are of major interest because they confirm and express precisely the fundamental prosomatic segmentation, as was explained in a prior publication (Lopez, A. 1978, op. cit.). Moreover, it appears that the genus *Metepeira* is exceptional among the Araneidae, in which coxal glands generally are poorly developed, being almost reduced to the sacculus and corresponding to Buxton's third and highest evolutionary stage in *Araneae verae* (Buxton, B. H. 1913, Zool. Jahrb., 14:231-282). The coxal glands of *Metepeira* are a peculiarity of the genus and not an evolutionary vestige. We will know more when further studies have been made into other genera of Araneidae and also into related families.

It is noteworthy that the coxal glands look histologically somewhat like the so-called "pharyngeal taste organ" (Millot, J. 1936, Bull. Soc. Zool. France, 61:27-38), mentioned above. This structure can no longer be regarded sensory but must be recognized as an exocrine gland opening into the pharyngeal cavity (personal observations in Oecobiidae and Hersiliidae). Its similarity to the cephalic coxal glands, especially in the genus *Metepeira*, and the results of parallel studies in *Uroctea* lead me to believe that they are perhaps all homologous.

There might be two hypotheses as to the actual role of coxal glands in the physiology of *Metepeira*, though neither is entirely convincing: 1) a filtering excretory function; 2) the secretion of a pheromone, if we consider the recently discovered opisthosomatic organs (Kovoor, J., Lopez, A. and Emerit, M. 1981. Proc. 6eme Coll. Arachnol. express. franç. Modena Pisa, Sept., 1981:53-60), the basic histological structures of which appear to be fairly closely related to those described here as coxal glands.

André Lopez, Laboratoire de Pathologie comparée (EPHE) et Laboratoire de Zoologie, Université des Sciences et Techniques du Languedoc, place E. Bataillon, 34 060, Montpellier, France.

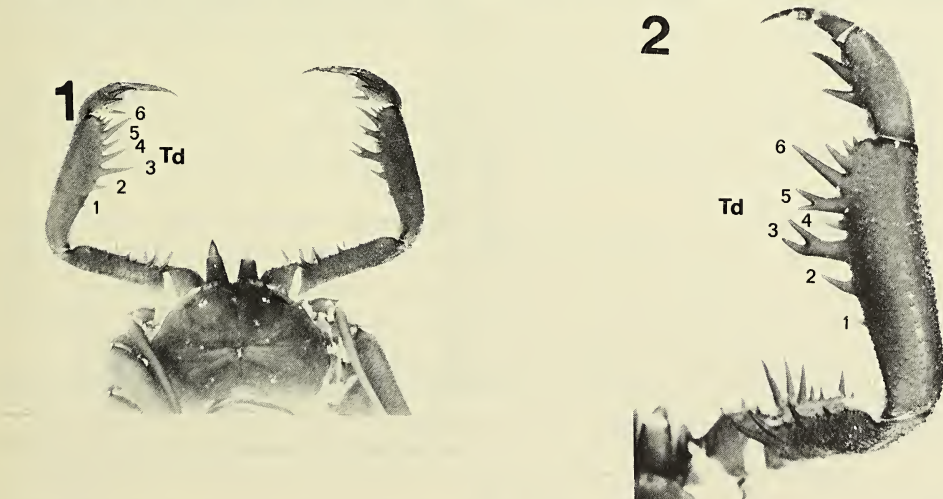
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**BIFID SPINES IN *PARAPHRYNUS AZTECA* (POCOCK)
(AMBLYPYGI: PHRYNIDAE)**

The spines on the pedipalps of amblypygids represent very important structures used for the capture of prey, holding it while proceeding to digest it, display threats, and during courtship interactions. Pedipalp spination has been used extensively for systematic studies in all members of this group as a very reliable character. Nevertheless, at the present stage of the knowledge of the group, nothing is known about the functional significance of the different spines, their homologies, the adaptive significance of different spine arrangements, what ontogenic changes they undergo and the basic abnormalities present in their development. During the course of examining several hundred specimens, I have found very few such abnormalities in pedipalp spination, and none, to my knowledge, has been reported in the literature.

A very unusual case of asymmetrical spine transformation into bifid apophysis has come to my attention and the present note serves to describe such a rare case and to review other abnormalities in spination previously noticed.

In a group of two males and three females of *Paraphrynus azteca* (Pocock) (Mex.: Palomares, Oaxaca, 24 July, 1909, A. Petrunkevitch, at AMNH), only one male presented dorsally on the right pedipalp tibia (Figs. 1 and 2) spines 3 and 5 transformed into bifid apophyses, and had normal spination on the left tibia. This abnormality reversed the length polarity in the two spines that characterize *Paraphrynus* species. Normally spine 5 is markedly shorter than spine 4 but on the abnormal right tibia, the bifid spine 5 is about double the size of the same spine on the opposite tibia, and spine 4 is about half the size of the normal spine. The male had both pedipalp tibiae of the same length, while having a shorter right femur 1 (18 mm) than the left (22 mm) but I have frequently found such asymmetries in leg one of *Paraphrynus* species. Although it is foreseeable that the presence of such asymmetries might possibly have unknown disadvantageous effects on the animal bearing them, the male now described had reached the longest pedipalp size in a sample of 20 specimens measured, which included specimens from both described forms,



Figs. 1 and 2.—*Paraphrynus azteca* (Pocock), male, dorsal view. Td, tibia dorsal.

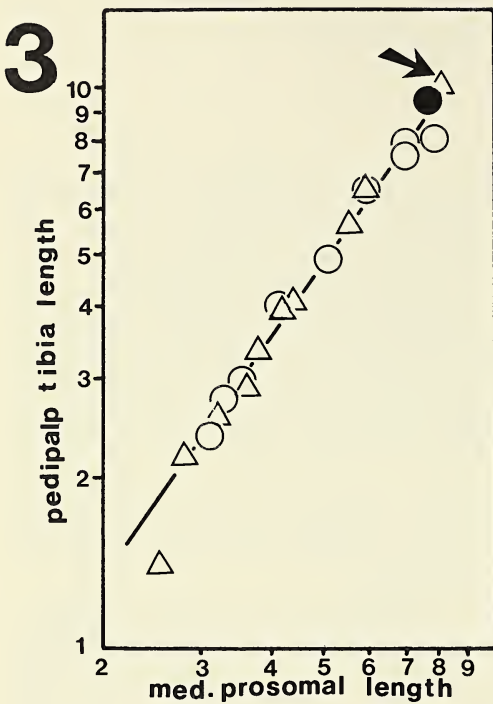


Fig. 3.—Allometric growth curve of pedipalp tibia length versus median prosomal length. All measurements in mm, $Y = 0.50 X^{1.4281}$. Black circle represents measurement of one specimen from syntype series (Tuxtla, Chiapas, Mexico).

Atoyac and Isthmus, (see arrow in Fig. 3). Its body length was 20.2 mm, whereas the longest known specimen (black circle, Fig. 3) measured 23 mm. Its abdomen appeared full which suggested it was a recently fed animal. A similar asymmetry, a bifid spine 3 on the right pedipalp tibia, was seen in a male of *Paraphrynus viridiceps* (Pocock) from New Providence Island, Bahamas (1913, C. J. Maynard, MCZ).

The bifid apophysis that characterizes *Musicodamon atlanteus* Fage at the distal end of the ventral pedipalp tibia, although superficially resembling the bifid spines presently reported of *Paraphrynus azteca*, might have evolved by the distal clustering of the ventral tibial distal spines on a common apophysis. Distal clustering of spines is characteristic of ontogenic changes occurring during pedipalp growth in members of the Phrynichidae and Damonidae but uncommon in Phrynidae.

An unnoticed abnormality in spine Td-3 appears in Fig. 2 of Rowland (1973, Assoc. Mex. Cave Studies, Bulletin, 5:123-128) in an unidentified species of *Paraphrynus* (*Tarantula* sp.), Td-3 is markedly shorter than Td-4 on the right pedipalp whereas on the left it has the normal size.

My sincere appreciation to Mr. Arthur Singer, AMNH, for his excellent photographic work and to Dr. Norman Platnick, AMNH, for providing me with laboratory facilities. This work was supported by a Fulbright-Hays Research award and was carried out at the American Museum of Natural History, New York. I am grateful to Dr. Lee H. Herman, Jr. for correcting my English and to Miss Tanya Clement for typing the manuscript.

Diomedes Quintero, Jr., Museo de Invertebrados, Estafeta Universitaria, Universidad de Panamá, República de Panamá.

SOBRE LA PRESENCIA DE *PHONEUTRIA BOLIVIENSIS* (F.O.P CAMBRIDGE) (ARANEAE, CTENIDAE) EN COSTA RICA

Las especies del género *Phoneutria* constituyen un grupo de arañas de interés para las ciencias médicas, por su veneno con fuerte acción neurotóxica en humanos y otros vertebrados (Bucherl, W. 1969. Mem. Inst. Butantan, 35:25-31).

El grupo es conocido únicamente de Sur América y sólo se ha mencionado fuera de este ámbito la presencia de una especie indeterminada en la costa atlántica de Costa Rica, en un informe sobre casos clínicos de aracnidismo por *Phoneutria* (Trejos, A. *et al.* 1971. Rev. Biol. Trop., 19 (1-2):241-249).

A pesar de que la taxonomía de *Phoneutria* presenta grandes confusiones (Bucherl, W. 1969. Mem. Inst. Butantan, 34:47-66) el trabajo de R. D. Schiapelli y B. S. Gerschman (1973. Rev. Soc. Ent. Argentina, (1-2):31-38) me ha permitido identificar esta especie como *P. boliviensis*, identificación corroborada por V. Dessimoni von Eickstedt (Instituto Butantan).

El Museo de Zoología de la Universidad de Costa Rica posee abundante material procedente de varias localidades de la zona atlántica (Limón, San Clemente, Guápiles, Turrialba), de las llanuras del norte (Venecia, Aguas Zarcas, Muelle, Canalete de Upala) y del litoral pacífico (San Isidro del General, Parrita, Golfito, Rincón, Isla del Caño) (Fig. 1).

Distribución geográfica.—*P. boliviensis* es conocida de las zonas tropicales de Bolivia, Perú, Ecuador y Colombia. En Costa Rica su distribución parece restringida a bosques de tierras bajas (menos de 600 m de altitud) y alta pluviosidad (más de 3000 mm anuales), llamados húmedos y muy húmedos en el sistema de zonas de vida de L. Holdridge. Estos



Fig. 1.—Mapa de Costa Rica y del occidente de Panamá mostrando la distribución aproximada del bosque tropical húmedo y muy húmedo (sistema de Holdridge) (punteado) y las localidades de colecta de *P. boliviensis* en Costa Rica (círculos). Se indica la posición de las ciudades de San José y Panamá (estrellas).

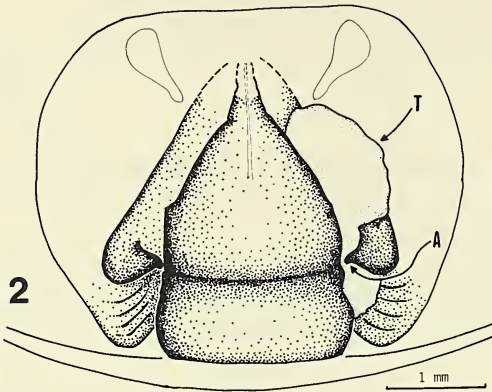


Fig. 2.—Epgiginio, vista ventral. A, apófisis unguliforme; T, Tapón postcopulatorio en el lado izquierdo del epiginio (el derecho fue removido).

bosques se continúan ininterrumpidamente desde las llanuras del norte y la región atlántica por el litoral panameño hasta Sur América. No así en la costa pacífica, en donde la población está ecológicamente aislada por las montañas altas del sistema de Talamanca y por una zona de bosque seco en la costa del Golfo de Panamá (Fig. 1). Sin embargo, este aislamiento no parece haber producido ninguna modificación aún, pues el análisis de los ejemplares del Pacífico no evidencia diferencias importantes con los del Atlántico.

Coloración.—Los ejemplares costarricenses de *P. boliviensis* presentan una coloración pardo rojiza en prosoma y patas; opistosoma amarillento con dos líneas oscuras longitudinales de puntos blancos en la región ventral (estos puntos blancos son también característicos de *P. colombiana*, especie de status incierto). También es muy conspicua en todos los ejemplares una línea negra en el dorso del tarso y la tibia del pedipalpo, así como una línea longitudinal oscura en el dorso del prosoma.

Tapón postcopulatorio.—Todas las hembras adultas colectadas en el campo poseen un tapón epigineal de considerables proporciones a cada lado de la barra central del epiginio (Fig. 2,T). Estos tapones se encuentran fuertemente adosados al epiginio y sostenidos por una apófisis unguliforme (Fig. 2,A) que se levanta en frente del orificio de entrada a la spermateca, el cual queda totalmente bloqueado. Otras especies de ctenidos de los géneros *Ctenus* y *Cupiennius*, de tamaño y hábitos similares a esta especie no presentan formaciones comparables a este tapón.

Carlos E. Valerio, Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica.

BOOK REVIEW

Spider Communication, mechanisms and ecological significance. Edited by P. N. Witt and J. S. Rovner. Princeton University Press, Princeton, New Jersey 08540. \$30.00, 441 pages, illustrated, 1982.

The book opens with a short introduction by Witt and Closes with a short epilogue by Rovner. Between, are nine chapters, each by an author (or two) whose researches have occupied the past 10 or 15 years. Whereas brief mention is made of the pioneering works in this field, one can see from the publications listed in the 40 pages of Literature Cited, that most, possibly 90%, of the contributions were published since the nineteen sixties. There is an index. Communication is discussed in its broadest sense, referring to any direct or indirect exchange of information. The mechanisms include visual, vibratory (transmitted through the substratum), acoustic, tactile, and pheromones, both airborne and contact. Each chapter closes with an indication of those questions for which future research may find answers.

Krafft, in his chapter, introduces us to the activities of various pheromones, particularly how these may function in the behavior of social spiders, his special research area. This includes not only the sexual pheromones, but others, such as that responsible for the mutual tolerance of one's conspecifics.

The next chapter, by Barth on vibrating signals, is the longest in the book (56 pages). The detailed anatomy of trichobothria and of slit sensillae, is described with illustrations. Evidence is presented to indicate that the trichobothria detect particle movement, airborne stimuli. The single slit just behind the tarsal claws apparently perceives sound, and the compound slit (or lyriform) organ at the distal end of the metatarsus is a vibration receptor. Much evidence as to how these organs function is adduced from the elegant experiments (some not heretofore published) described in this chapter.

Uetz and Stratton discuss acoustic communication, of which they consider three types. Best known is stridulation, and they supply a drawing showing the different places on a spider's body where stridulating organs may be found. That percussion too is used by many spiders has been known for many years, but that some spiders may produce sounds by the vibration of a leg (as bee or fly wings do) is a recent discovery. While the use of sounds is best known to us in courtship behavior, it is pointed out that sound may be involved in agonistic behavior too. It has also been shown that for species related morphologically, and which may even have identical genitalia, the sounds made during courtship are different. Interbreeding presumably does not occur because of this difference.

In Lyn Forster's chapter on visual communication in salticids she first supplies detailed descriptions of the eye anatomy, based principally on the work of Homann and of Land. She also goes into great detail in describing the many events during courtship, step by step. It is further pointed out "that the popular assumption that jumping spiders uniformly enjoy bright sunlight is mistaken, and that many live in very dimly lit habitats."

Most of Jackson's chapter is devoted to summarizing his researches on *Phidippus johnsoni*. These have been very extensively reported in detail, and from the literature list

one can see that from 1976 through 1981 he has published 14 papers on this species. As Jackson points out, other sensory modalities (auditory and olfactory) may play a part as well as visual, and he has shown that even a non-visual courtship (his type two) may occur.

The chapter by Tietjen and Rovner is concerned principally with chemical coordination in lycosids. Presumably the receptors include the tarsal organ, and also the curved, blunt-tipped steeply inserted hairs found concentrated on the distal portion of the appendages, being especially abundant on the male pedipalp. Besides the pheromone made by females which incites the male to court, there may even be one produced by males which enables recognition of conspecifics, so that the female's predatory behavior is inhibited.

The chapter by Riechert on communication versus coercion concerns intraspecific competition (for mates, for space territoriality, and rank position). The mechanisms are best known in *Agelenopsis aperta*.

Bergess and Uetz supply the chapter on social spacing strategies. This includes close aggregations which may be temporary (as in hibernating; with spiderlings; and the mother-spiderlings association) or those which are regularly social. Different stimuli may be involved, vibrating signals being most commonly used. In some species conspecifics are tolerated at closer distances in areas where food is abundant. Most employ agonistic behavior like leg jerking and web shaking to maintain space. Rovner's recent work with lycosids has shown that tactile stimuli are provided to the offspring by the special spiny knobbed abdominal hairs of the mother.

The final chapter, by Riechert and Luczak, concerns behavioral responses to prey. This includes "valuable information on spider behavior and ecology that applies some of the material discussed earlier [in this book] on sensory physiology and modes of signalling." All araneologists will find the book of interest; those working with the ecology and ethology of spiders will find it especially useful.

B. J. Kaston, Department of Zoology, San Diego State University, San Diego, California 92182

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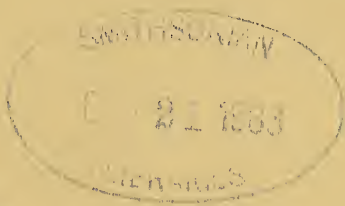
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THE ERIGONINE SPIDERS OF NORTH AMERICA.
PART 6.¹ THE GENUS *WALCKENAERIA* BLACKWALL
(ARANEAE, LINYPHIIDAE)

A. F. Millidge

Little Farthing, Upper Westhill Road,
Lyne Regis, Dorset DT7 3ER, England

ABSTRACT

A survey is reported of the North American species of the erigonine genus *Walckenaeria* s.lat. *Erigone* (*Minyriolus*) *castanea* Emerton, *Sisicottus cornuellus* Chamberlin and Ivie and *Sisis saniuana* Chamberlin and Ivie are transferred to *Walckenaeria*. The following synonyms are proposed: *Cornicularia varipes* Banks = *W. communis* (Emerton); *Lophocarenum* (*Mythoplastoides*) *abruptum* Emerton = *W. atrotibialis* O. P.-Cambridge; *Trachynella longidens* Holm = *W. castanea* (Emerton); *W. vidua* Wunderlich = *W. capito* (Westring); *Heteroprosopotheca* Wunderlich = *Walckenaeria* Blackwall; *Kas-tonia* Wunderlich = *Microcornicularia* Wunderlich; *Pseudocornicularia* Wunderlich = *Microcornicularia* Wunderlich. *W. karpinskii* auct. is not *W. karpinskii* O. P.-Cambridge, and is renamed *W. holmi*. *Cornicularia selma* Chamberlin and *Tigellinus mesus* Chamberlin are excluded from the genus. *Walckenaeria* can be defined on the basis of somatic characters, and on the form of the palpal organs, but definition on the basis of the female genitalia has not been possible. The genus now comprises 76 species in N. America, including the following 49 new taxa: *W. aenea*, *W. anceps*, *W. aprilis*, *W. arcana*, *W. arctica*, *W. aurata*, *W. bifida*, *W. blanda*, *W. carolina*, *W. clavipalpe*, *W. columbia*, *W. crocea*, *W. discolor*, *W. dondalei*, *W. emarginata*, *W. exigua*, *W. faceta*, *W. fallax*, *W. floridiana*, *W. fraudatrix*, *W. fusciceps*, *W. gertschi*, *W. helenae*, *W. holmi*, *W. iviei*, *W. latens*, *W. maesta*, *W. mexicana*, *W. microspiralis*, *W. occidentalis*, *W. oregona*, *W. palustris*, *W. pallax*, *W. prominens*, *W. puella*, *W. pullata*, *W. reclusa*, *W. redneri*, *W. rufula*, *W. rutilis*, *W. septentrionalis*, *W. serrata*, *W. solivaga*, *W. subdirecta*, *W. subpallida*, *W. subspiralis*, *W. subvigilax*, *W. tenella*, *W. teres*. The species are assigned to nine species groups, several of which appear to be endemic to N. America. Descriptions, diagnoses and distribution maps are given for each species.

INTRODUCTION

The genus *Walckenaeria* was erected by Blackwall (1833) for the European species *W. acuminata* and *W. cuspidata* Bl. The original spelling of the name was as given above, but Blackwall (1841) changed the name to *Walckenaera*, and this spelling was used in the arachnological literature for a century or more (see Bonnet 1959:4807). Despite the long usage of the spelling *Walckenaera*, the I.C.Z.N. Rules (Art. 32[a]) require a return to the original spelling, and this is being adopted by recent authors.

The N. American species included in the genera *Cornicularia* Menge and *Tigellinus* Simon (now transferred to *Walckenaeria*), and in *Walckenaeria* itself, were described by Crosby and Bishop (1931). Wunderlich (1972) has published a review of the genus *Walckenaeria* which covers the European species and some N. American and Nepalese species.

¹ For Part 5 of this series, see Bull. Amer. Mus. Nat. Hist., 170:242-253.

GENUS *WALCKENAERIA* BLACKWALL

Walckenaeria Blackwall 1833:105; Roewer 1942:668; Wund

Walckenaeria Blackwall 1833:105; Roewer 1942:668; Wunderlich 1972:371. Type species *W. acuminata* Bl. by first species rule.

Walckenaera Blackwall 1841:219; Simon 1884:813 and 1926:413, 507; Crosby and Bishop 1931:378; Locket and Millidge 1953:191; Bonnet 1959:4807; Wiehle 1960:105.

Wideria Simon 1864:477; Simon 1884:799 and 1926:405, 504; Roewer 1942:669; Locket and Millidge 1953:193; Bonnet 1959:4817; Wiehle 1960:110. type species *Theridion anticum* Wider by first species rule.

Cornicularia Menge 1868:226; Simon 1884:843 and 1926:417, 508; Crosby and Bishop 1931:359; Roewer 1942:660; Locket and Millidge 1953:204; Bonnet 1956:1219; Wiehle 1960:142. Type species *Walckenaera unicornis* O.P.-Cambridge by monotypy.

Spiropalpus Emerton 1882:39. Type species *Spiropalpus spiralis* Emerton by monotypy.

Prosopotheca Simon 1884:829; Simon 1926:414, 507; Roewer 1942:664; Locket and Millidge 1953:201; Bonnet 1958:3781; Wiehle 1960:159. Type species *Theridion monoceros* Wider by designation.

Tigellinus Simon 1884:828; Simon 1926:414, 507; Crosby and Bishop 1931:377; Roewer 1942:666; Locket and Millidge 1953:204; Bonnet 1959:4620; Wiehle 1960:176. Type species *Phalops furcillatus* Menge by monotypy.

Trachynotus Dahl 1886:95; Simon 1926:412, 506. Type species *Walckenaera obtusa* Bl. by monotypy.

Trachynella Braendegaard 1932:19 (*nom. nov.* for *Trachynotus* *praeocc.*); Roewer 1942:667; Locket and Millidge 1953:199; Bonnet 1959:4674; Wiehle 1960:169.

Definition.—This genus is composed of spiders with a total length of 1.35-4.0 mm. The female carapace is usually unmodified, but is occasionally distinctly raised anteriorly (e.g. Fig. 101). The male carapace in many species carries a lobe (e.g. Figs. 98, 188) or a horn (e.g. Figs. 142, 267); where there is a lobe, this carries the posterior median eyes. The males of many of the N. American species have the carapace unmodified. The male horns of some N. American species are furnished with spatulate hairs, which under high magnification are seen to be trifurcate (Fig. 305). Each of these trifurcate hairs arises from a deep pit on the horn (Fig. 306); these pits may possibly have the same function as the cephalic holes in other male erigonines, that is, to secrete sexual pheromones (Blest and Taylor 1977). The horn has been broken off in a number of the males examined, and this is probably evidence that the female grasps the horn during mating. There are somewhat similar trifurcate hairs on the turret of the type species (Wiehle 1960: Fig. 183c) and in some other European species (Kronestedt 1980: Figs. 1-3). There is a file on the lateral margins of the chelicerae in both sexes; the spacing of the striae is sometimes of taxonomic importance. The sternum is longer than wide, with the ratio length/width at least 1.1:1. The pedicel is distinctly sclerotized, more so than in most erigonine genera, and is quite conspicuous in a few species (Fig. 167). The abdomen is without scuta and is normally unicolorous. The European and practically all the N. American species have the tibial spines 2211 in both sexes; the spines are slender and are often less developed in the male, particularly on legs I-II. In one American species (*W. aenea*) and in some central African species, however, the tibial spines are 1111 (Holm 1962:176; Locket and Russell-Smith 1980:69). All the metatarsi have a trichobothrium; the value of TmI for the N. American species lies in the range 0.35-0.75. The superior tarsal claws of legs I-II, and often of leg III, are relatively large and strongly pectinate (Figs. 111, 112); the claws on leg IV have the teeth greatly reduced. The number of teeth on the anterior claws varies from species to species.

The palpal tibia of the male is drawn out distally into an apophysis of variable form, and in some species there are additional apophyses. The palpal tibia of both sexes has 3 trichobothria; in one species (*W. saniuana*) the number is reduced to 2 in the male. The paracymbium of the male palp has a simple horseshoe shape. The haematodocha of the palpal bulb is clearly visible on the mesal side (Figs. 1, 3), and often also on the ectal side (e.g. Fig. 78). The subtegulum and tegulum offer no peculiarities. The suprattegulum curves downwards, away from the cymbium (Figs. 1, 2, 3, 5, 7), and this extension (suprattegular apophysis, SA) often terminates in a dark colored point. A membranous apophysis, originating at the stalk but attached also to the SA, runs partway down the mesal side of the SA before passing over to the ectal side; the terminal part of the membrane then curves upwards, and in the living spider supports the distal part of the embolus. The embolic division (ED) of the palp comprises a simple tailpiece and a coiled embolus of about 1.5-2 turns (e.g. Fig. 9); the embolus is a flat ribbon, at least basally, with a thickened black sclerotized margin. The female epigynum exhibits considerable variability in external appearance. In the majority of the species, the epigynum is enclosed by a simple plate through which the outlines of the apodemes, the spermathecae and the internal ducts are visible (e.g. Fig. 15). The openings to the spermathecal ducts lie in a small depression, or sometimes 2 depressions, which are difficult to see. In a few species, however, there are two tongue-like plates arising from the epigynal surface (e.g. Fig. 278); in these species, the openings to the ducts appear to lie beneath the plates. Internally the spermathecal duct passes from the spermatheca towards the median line by a curved pathway of varying complexity, and then runs posteriorly in a curve to the openings; the two curved, pincer-like ducts leading to the genital openings (e.g. Figs. 25, 178) often give a characteristic appearance to the epigynum. The length of the internal duct shows a good deal of variation, the length often showing some correlation with the length of the male embolus. The anterior portion of the duct, particularly where this is long, appears to lie along the margins of a twisted lamella (Figs. 22, 105) which is attached to the spermatheca and apodeme. In a few species, the duct passes to the lateral side of the spermatheca before curving back to the median line and the openings (Figs. 290, 297).

The male palpal organs *Walckenaeria* have a constant form throughout the genus, and this can be regarded as a derived character which supports the hypothesis that the genus is monophyletic. There are, however, several genera in which the palpal structure is very close to that of *Walckenaeria*; in particular the myrmecophilous genus *Evansia* O.P.-Cambridge and the genera *Moebelia* Dahl, *Minyriolus* Simon and *Typhochrestus* Simon (Merrett 1963:462). The female genitalia have a somewhat variable form, and no common character which can be used to define the genus has been identified. *Walckenaeria* is one of the few erigonine genera which can be defined and diagnosed by somatic characters. Other erigonine genera may have strongly pectinate tarsal claws, but the combination of this character with the elongated sternum seems to be present only in *Walckenaeria*.

Synonymy.—Most of the previously described species now included in the genus *Walckenaeria* have in the past been assigned to other genera, particularly to *Cornicularia*, *Wideria*, *Prosopotheca*, *Tigellinus* and *Trachynella*. These genera were defined principally on eye characters and on the form of the male carapace (Simon 1894). It was pointed out (Locket and Millidge 1953:191; Miller 1959:56) that these genera were rather artificial, and that the species should probably be united into the single genus *Walckenaeria*. In his revision of this genus, Wunderlich (1972) reduced *Cornicularia*, *Wideria*, *Prosopotheca*

and *Tigellinus* to the status of subgenera, with *Trachynella* regarded as a synonym of the nominate subgenus *Walckenaeria*. He also erected a number of new subgenera.

Species transferred to *Walckenaeria*: The N. American species previously placed in *Cornicularia*, *Tigellinus* and *Prosopotheca* have been transferred into *Walckenaeria*. On the basis of the genitalia, the pectinate tarsal claws and the elongated sternum, the species *Minyriolus castaneus* (Emerton), *Sisis saniuana* Chamberlin and Ivie and *Sisicottus cornuella* Chamberlin and Ivie have also been transferred to *Walckenaeria*. *Lophocarenum abruptum* Emerton, placed in *Mythoplastiodes* by Crosby and Bishop (1933) and in *Entelecara* by Hackman (1954), is a synonym of *Walckenaeria atrotibialis* O.P.-Cambridge, and is included in this paper under that name (see *W. atrotibialis* description).

Species excluded from *Walckenaeria*: The following species have not been included in this study.

Cornicularia selma Chamberlin (1948:526). This species was based on two females from Oregon, but these have not been traced. The figure given for the epigynum indicates that the species is probably not a *Walckenaeria*.

Prosopotheca transversa Crosby. According to Crosby and Bishop (1931) this species was based on an immature female of *Tennesseellum formicum* (Emerton).

Tigellinus mesus Chamberlin (1948:556). This species was based on a single female from Colorado, but the specimen cannot be found. The figure given for the epigynum indicates that the species is probably not a *Walckenaeria*.

Tigellinus (?) *perditus* Chamberlin (1948:555). This species was based on two females of uncertain origin, and the specimens cannot be found. This species is almost certainly a *Walckenaeria*, and the epigynum is similar to that of one of the species described in this paper. In the absence of Chamberlin's specimens, however, it has not been possible to include the species in the present study.

Species and species groups.—In N. America the genus *Walckenaeria* comprises 76 known species (Tables 1-3); there can be little doubt that with future discoveries this number will approach 100. I have split the species into nine species groups, which are based mainly on the form of the male carapace and on the male genitalia. Definition of the groups on the basis of the epigyna is not very satisfactory; the epigynal differences in many cases lie more in the visual appearance than in any basic difference in form, and the differences can be indicated only by figures. The species groups given in this paper are in substantial agreement with the subgenera proposed by Wunderlich (1972), but because of the uncertainties involved in defining these groups I regard it as preferable at the present time not to regard them as formal named subgenera. The species groups used are defined as follows.

1. *acuminata* Group (based on *W. acuminata* Bl.)

The male carapace may have a lobe which carries the posterior median eyes; in most N. American species, however, the carapace is unmodified. The palpal tibia usually bears a single apophysis of the general form shown in Figs. 67-70, but there is an additional lateral apophysis in some species (e.g. Figs. 72, 87). The SA ends in a simple blunt point (Fig. 1) which is usually not visible in the unexpanded palp. The embolic coil can be very large (Fig. 8) to small (Fig. 123). The female epigynum has the anterior area either clear of markings (Fig. 127) or carries the outlines of long ducts (e.g. Figs. 15, 38). This group is equivalent to the nominate subgenus *Walckenaeria* (Wunderlich 1972), of which *Heteroprosopotheca* Wunderlich is a synonym (NEW SYNONYM: see *W. capito*). This group is distributed throughout the northern hemisphere.

2. *directa* Group (based on *W. directa* [O.P.-Cambridge])

The male carapace carries anteriorly a horn (Fig. 142) or other modification (e.g. Fig. 147), which is clothed at least in part with conspicuous spatulate hairs (Fig. 303); the *tibialis* group have a similar horn. The palpal tibia is as shown in Figs. 168-171; a few species in the *minuta* group have rather similar tibiae. The SA terminates in a lightly sclerotized sickle-shaped appendage (Fig. 137); the membraneous part arising mesally from the stalk is strongly developed to give a sheet-like structure on the ectal side (Figs. 133, 135, 138). The embolic coil is of medium size (Fig. 135). The female epigynum is of the form shown in Figs. 175, 176; all the species except *W. carolina* (Fig. 177) have closely similar epigyna. This group corresponds with the subgenus *Pseudoprosopotheca* Wunderlich, except that *W. tibialis* and *W. tumida* are excluded. The group appears to be endemic to N. America.

3. *tibialis* Group (based on *W. tibialis* [Emerton])

The male carapace has a short, stout horn (Fig. 146) clothed anteriorly with spatulate hairs. The palpal tibia is as shown in Figs. 172-174. The SA terminates in a curved spike and the embolic coil is small in size (Figs. 182-185). The female epigynum is as shown in Figs. 179, 180. This group seems to be endemic to N. America.

4. *tricornis* Group (based on *W. tricornis* [Emerton])

The male carapace has a lobe, which is forked anteriorly (Figs. 188, 189) and carries the PM eyes. The palpal tibia has a lateral apophysis which differs from species to species (Figs. 194-202). The SA terminates in a black sclerotized part which may be forked distally, and the embolic coil is of medium size (Fig. 186). The female epigynum has two forms (e.g. Figs. 203, 210). There are no representatives of this group in Europe, but it is possible that some of the central African "*Tigellinus*" species (Holm 1962) are related; certainly some of the female genitalia figured by Holm appear similar to those of the N. American species. This group corresponds with the subgenus *Pseudotigellinus* Wunderlich.

5. *minuta* Group (based on *W. minuta* [Emerton])

The male carapace has a horn of variable form (e.g. Figs. 229, 238) arising from the ocular area. The palpal tibia has two apophyses (Figs. 221-228), the lateral one having stiff black bristles along the margin in some species. The SA terminates in a black spike, which is clearly visible on the ectal side (Figs. 213-217), and the embolic coil is of medium size (Fig. 213). The female epigynum has two forms (Figs. 242, 246), but the internal genitalia are of a similar pattern in all the species (Figs. 250-253). This group corresponds with the subgenus *Microcornicularia* Wunderlich. *Pseudocornicularia* Wunderlich (type species *W. thrinax*) and *Kastonia* Wunderlich (type species *W. pinocchio*) become synonyms of *Microcornicularia* — NEW SYNONYMS. On present knowledge this group is endemic to N. America, but the E. African species *Walckenaeria (Tigellinus) meruensis* Tullgren (known only from the female: Holm 1962) has the epigynum and internal genitalia very similar to those of the N. American species in this group (Fig. 248, cf. Holm's Plate 6, Figs. 12, 13, and Figs. 250, 252 cf. Holm's Fig. 72).

6. *unicornis* Group (based on *W. unicornis* [O.P.-Cambridge])

The male carapace has a broad horn within the ocular area (Figs. 267-272); this horn is quite different in form from that of the *directa* group, and is not clothed with spatulate hairs. The palpal tibiae have two long apophyses lying contiguous to one another (Figs. 255, 256, 262). The SA terminates in a dark colored point (Figs. 3, 5, 257), which is not visible in the unexpanded palp, and the embolic coil is of medium to large size (Figs. 254,

259). The female epigynum has two forms (Figs. 273-275 and 278-283). This group corresponds with the sub-genus *Cornicularia* (Wunderlich 1972), and is widely distributed throughout the northern hemisphere.

7. *cuspidata* Group (based on *W. cuspidata* Bl.)

The male carapace has a tiny prominence in the ocular area (Figs. 285, 286). The palpal tibia (Fig. 287) is rather similar to those of the *acuminata* group. The SA has a short trunk-like extension distally (Fig. 7), and the embolic coil is fairly large in diameter (Fig. 284). The female epigynum (Fig. 288) is quite distinct from those of the other groups, and the internal ducts follow a different pathway (Fig. 290). This group contains a single species (with the N. American population regarded here as a subspecies), and corresponds with the subgenus *Heteroprosopotheca* Wunderlich. The distribution is holarctic.

8. *atrotibialis* Group (based on *W. atrotibialis* O.P.-Cambridge)

The male carapace has a shallow lobe anteriorly, and the clypeus is strongly projecting (Fig. 293). The palpal tibia has two apophyses of approximately equal size (Fig. 294). The SA terminates in a short point, not visible in the unexpanded palp, and the embolic coil is rather small in diameter (Fig. 292). The epigynum (Fig. 295) is characteristic, and the internal ducts follow a course reminiscent of that in *W. cuspidata*. This group comprises a single species, and corresponds with the subgenus *Parawideria* of Wunderlich. The distribution is holarctic.

9. *antica* Group (based on *W. antica* [Wider])

The male carapace has a lobe or lobes anteriorly. The palpal tibia has two apophyses, the lateral being of rounded form. The SA ends in a blunt point, and the embolic coil is of medium size. The female epigynum and the internal genitalia are of fairly distinctive appearance (Figs. 298, 300) (see also Wunderlich 1972, and Kronestedt 1980). This group corresponds with the subgenus *Wideria* (Wunderlich 1972). The group is widely distributed in Europe and probably Asia, but *W. fraudatrix* is the first species of the group to be recorded from N. America.

The genus *Walckenaeria* in N. America presents some interesting taxonomy, with the differences between the species often small, and sometimes not visible in the female by external examination of the spider. The common species *W. spiralis* auct. is a complex of at least three sibling species (*W. spiralis*, *W. subspiralis* and *W. microspiralis*), which have identical palpal organs and which can be distinguished in the female only by the form of the internal genitalia (see *W. spiralis* diagnosis). Previous records for *W. spiralis* are consequently unreliable. The *acuminata* group of species has undergone vigorous speciation in N. America, and in addition to the *W. spiralis* siblings the group contains many other closely related species (usually identified as "*W. spiralis*" in the collections) which can be distinguished in the female sex only by examination of the internal genitalia.

In the *directa* species group, *W. directa* and its sibling *W. subdirecta* cannot be distinguished by their genitalia, but only by the spacing of the striae of the cheliceral file (see *W. directa* diagnosis). The differences in the file are perfectly clear (Figs. 308-311), and although there are small variations in this character, as in most others, there is no overlap between the two species, which on a few occasions have been sympatric. Previous records for *W. directa* must also be regarded as unreliable. A similar situation exists with the two species *W. pallida* and *W. subpallida*. The common species *W. communis*, on the other hand, has the spacing of the cheliceral striae more or less constant over the whole geographical range of the species, and no siblings have been detected. van Helsdingen (1963:

35) drew attention to the differences in the cheliceral files of several closely related *Lepthyphantes* species, and it has been suggested that the differing files may play some part in species isolation (van Helsdingen, Thaler and Deltshev 1977:45). The pattern of vibrations produced by rapid movement of the palpal femur along the file would be dependent on the spacings of the file, and the wave-form (“tune”) of the vibrations could serve as a recognition code between the sexes prior to mating.

Distribution and natural history.—The genus *Walckenaeria* is distributed throughout the whole of the northern hemisphere, with records from beyond the arctic circle to the equator. In the East African mountains the genus extends marginally below the equator, but I know of no other certain records from the southern hemisphere. The distribution maps given for the species in this paper are based only on the material actually examined, that is, published records have been ignored unless I have seen the specimens. As with distribution maps from other countries, it must be accepted that the maps often tend to reflect the distribution of collecting arachnologists (past and present) and of favoured collecting areas rather than the true range of the species. As with most erigonines, the *Walckenaeria* species live mostly at ground level, often in damp situations, though some, as adults, may move up into low shrubs. The habitats given under the species descriptions are limited in most instances to those recorded in the vials examined.

DESCRIPTION OF THE SPECIES

The species are described in the order given in Tables 1-3. All figures of palps are of the right palp, unless stated to the contrary. The holotypes of the new species are deposited in AMNH, CNC or MCZ, as given under the species description.

acuminata Group

This group contains a large number of species, which in most instances can be distinguished only by their genitalia. Because of the small differences which sometimes separate the species, it has not been possible to devise keys which are wholly satisfactory or wholly reliable, particularly for females.

Partial keys to the species

Males

- 1. Carapace with large lobe (Fig. 98). *capito*
Carapace with small lobe (Fig. 113) *castanea*
Carapace with no lobe 2
- 2. Palpal tibia with small lateral apophysis (Figs. 72, 87-90) 3
Palpal tibia without a lateral apophysis 4
- 3. Palpal tibia as Fig. 72 *redneri*
Palpal tibia as Figs. 87-90
. *dixiana, floridiana, digitata, maesta, mexicana* (see species descriptions)
- 4. Carapace bright orange, abdomen pale; southern species (Mexico). 5
Color less striking 6

5. Palpal tibia Fig. 82. *aenea*
 Palpal tibia Figs. 76, 81 *gertschi*
 Palpal tibia Figs. 80, 83, 85, 96 *iviei*, *rutilis*, *crocea* (see species descriptions)
6. Embolic coil very large; SA with "hook" anteriorly (Fig. 8); palpal tibia Fig. 67
 *spiralis*, *subspiralis*, *microspiralis*, (see species descriptions)
 Embolic coil less large 7
7. Embolic coil slightly smaller than in *spiralis*; SA with notch but no "hook" anteriorly
 (Fig. 55) *pellax*
 Embolic coil smaller than in Fig. 55 8
8. Embolic coil moderately large (Figs. 57, 59) *fallax*, *subvigilax* (see species descriptions)
 Embolic coil somewhat smaller (Figs. 10, 12, 65) 9
9. Carapace, sternum and legs fairly bright orange and brown; distribution southern
 (Mexico) *rufula*
 Carapace less brightly colored; distribution northern or western
 *arctica*, *saniuana* (see species descriptions)

Table 1.—N. American *Walckenaeria* species: *acuminata* species group. The species are described in the text in the order given.

<i>W. spiralis</i> (Emerton)
<i>W. subspiralis</i> , new species
<i>W. microspiralis</i> , new species
<i>W. arctica</i> , new species
<i>W. sanjuana</i> (Chamberlin and Ivie), new combination
<i>W. latens</i> , new species
<i>W. arcana</i> , new species
<i>W. pullata</i> , new species
<i>W. discolor</i> , new species
<i>W. faceta</i> , new species
<i>W. pellax</i> , new species
<i>W. fallax</i> , new species
<i>W. subvigilax</i> , new species
<i>W. iviei</i> , new species
<i>W. rutilis</i> , new species
<i>W. rufula</i> , new species
<i>W. crocea</i> , new species
<i>W. gertschi</i> , new species
<i>W. aenea</i> , new species
<i>W. capito</i> (Westring)
<i>W. redneri</i> , new species
<i>W. clavipalpe</i> , new species
<i>W. castanea</i> (Emerton), new combination
<i>W. dixiana</i> (Chamberlin and Ivie), new combination
<i>W. floridiana</i> , new species
<i>W. digitata</i> (Emerton), new combination
<i>W. maesta</i> , new species
<i>W. aurata</i> , new species
<i>W. mexicana</i> , new species
<i>W. puella</i> , new species
<i>W. blanda</i> , new species

Females

1. Carapace distinctly raised anteriorly (Fig. 101); epigynum Fig. 93 *capito*
Carapace not significantly raised. 2
2. Palpal tibia/tarsus distinctly swollen (Fig. 118); epigynum Fig. 95 *clavipalpe*
Palpal tibia/tarsus not of this form 3
3. Brightly colored spiders, with carapace bright orange, abdomen grey to white, legs orange/brown; southern species (Mexico). 4
Spiders less strikingly colored 5
4. Epigyna Figs. 37, 38 *iviei, rutilis* (see species descriptions)
Epigynum Fig. 91 *gertschi*
Epigynum Fig. 92 *aenea*
5. Epigynum Fig. 94 *redneri*
Epigynum Fig. 96 *castanea*
Epigynum not as Figs. 94, 96. 6
6. Epigynum relatively simple, with internal ducts not visible (Figs. 33, 127-132)
. . . *dixiana, floridiana, digitata, maesta, aurata, puella, pullata* (see species descriptions)
Epigynum with ducts visible in central area, both anterior and posterior to the spermathecae (Figs. 14-21, 34-38). Note: occasionally in dark colored specimens of *spiralis* and its siblings the ducts are scarcely if at all visible 7
7. Epigynum Fig. 35 *blanda*
Epigynum not as Fig. 35. 8
8. Species with distinctly southern distributions (e.g. Mexico).
. *arcana, discolor, faceta* (see species descriptions)
Species with distributions mainly northern and/or western
. . . *spiralis, subspiralis, microspiralis, arctica, saniuana, latens* (see species descriptions)

Walckenaeria spiralis (Emerton)

Figs. 2, 4, 8, 9, 14, 15, 16, 22, 23, 28, 67, 109, 112; Map 1

Spiropalpus spiralis Emerton 1882:39.*Cornicularia spiralis*: Roewer 1942:664.*Walckenaera vigilax*: Crosby and Bishop 1931:378; Kaston 1948:206 (misidentification: *nec Neriene vigilax* Blackwall).*Cornicularia vigilax*: Bonnet 1956:1227 (misidentification).*Walckenaera spiralis*: Dondale and Redner 1972:1644.

This species was confused with *W. vigilax* (Blackwall) by Crosby and Bishop (1931) and some subsequent authors; this error was pointed out by Fage (1938:373) and corrected by Dondale and Redner (1972). *W. spiralis* has not previously been differentiated from *W. subspiralis*, *W. microspiralis* and some other closely related species; hence most previous records for *W. spiralis* are suspect.

Type.—Two female and two male syntypes from New Haven, Connecticut, October 1881; in Emerton Collection, MCZ, examined.

Table 2.—N. American *Walckenaeria* species: *directa*, *tibialis* and *tricornis* species groups. The species are described in the text in the order given.

directa group

- W. directa* (O. P.-Cambridge)
- W. subdirecta*, new species
- W. communis* (Emerton)
- W. breviaria* (Crosby and Bishop)
- W. pallida* (Emerton)
- W. subpallida*, new species
- W. prominens*, new species
- W. indirecta* (O. P.-Cambridge)
- W. oregona*, new species
- W. dondalei*, new species
- W. brevicornis* (Emerton)
- W. carolina*, new species

tibialis group

- W. tibialis* (Emerton)
- W. tumida* (Crosby and Bishop)
- W. teres*, new species

tricornis group

- W. tricornis* (Emerton)
 - W. palustris*, new species
 - W. aprilis*, new species
 - W. solivaga*, new species
 - W. anceps*, new species
 - W. bifida*, new species
 - W. serrata*, new species
 - W. weber* (Chamberlin), new combination
 - W. occidentalis*, new species
 - W. helenae*, new species
 - W. reclusa*, new species
 - W. septentrionalis*, new species
 - W. columbia*, new species
-

Description.—Total length: female 2.0-2.6 mm, male 1.9-2.2 mm. Carapace: length: female 0.9-1.0 mm, male 0.85-0.95 mm. Orange-brown to brown, often darkened anteriorly; male carapace not raised behind the eyes (Fig. 109). Chelicerae: the lateral striae are moderately widely spaced in both sexes. Abdomen: black. Sternum: orange-brown, suffused with black particularly on margins. Legs: orange to orange-brown. TmI: female 0.55-0.58, male 0.50-0.55. Male palp: Figs. 2, 4, 8, 9, 67; the embolic coil is large, and the SA has a distinct hook-like projection anteriorly. Epigynum: Figs. 14, 15, 16. Externally the appearance is variable, depending on the transparency of the integument; sometimes the spermathecae are only faintly visible, while occasionally the internal structure is much clearer (Fig. 16). Internally, the duct leaves the spermatheca via a double spiral (Fig. 23) inside a dark colored screw-shaped extension of the spermatheca (Fig. 28); thereafter the duct (observable after clearing the epigynum) follows an irregular serpentine course, probably along the margins of a twisted lamella, to the external opening (Fig. 22).

Diagnosis.—Males of *W. spiralis* and *W. subspiralis*, which are structurally indistinguishable, are diagnosed by the large diameter of the embolic coil (Fig. 8), coupled with the form of the SA, which has a hook-like projection anteriorly. The palp of *W. spiralis* is also indistinguishable from that of *W. microspiralis*, and males of *W. spiralis/subspiralis* can be

Table 3.—N. American *Walckenaeria* species: *minuta*, *unicornis*, *cuspidata*, *atrotibialis* and *antica* species groups. The species are described in the text in the order given.

minuta group

- W. minuta* (Emerton)
- W. exigua*, new species
- W. tenella*, new species
- W. thrinax* (Chamberlin and Ivie)
- W. cornuella* (Chamberlin and Ivie), new combination
- W. monoceras* (Chamberlin and Ivie)
- W. pinocchio* (Kaston)
- W. placida* (Banks)
- W. emarginata*, new species

unicornis group

- W. auranticeps* (Emerton)
- W. ledpia* (Kulczynski)
- W. fusciceps*, new species
- W. clavicornis* (Emerton)
- W. holmi*, new species

cuspidata group

- W. cuspidata brevicula* (Crosby and Bishop), new status

atrotibialis group

- W. atrotibialis* O. P.-Cambridge

antica group

- W. fraudatrix*, new species
-

distinguished from *W. microspiralis* only by a difference in the value of TmI (0.50-0.55 for *W. spiralis/subspiralis*, cf. 0.65 for *W. microspiralis*); it is not certain that this difference is constant. The carapace of *W. microspiralis* is slightly more raised behind the eyes than in *W. spiralis* (Fig. 110 cf. Fig. 109), but the difference is small and probably not reliable for diagnosis. The epigynum of *W. spiralis* (Figs. 14, 15, 16) can be similar to that of several other species in this group, and the form of the internal genitalia offers the only reliable means of diagnosis. The spermathecae have a long screw-like extension (Fig. 28), inside which the duct follows a double spiral path of 3-4 turns in each direction (Fig. 23); this character distinguishes *W. spiralis* from all other *Walckenaeria* species. The form of the spermathecal extension can be seen without clearing, by lifting the epigynum and observing the dorsal side thus exposed (Fig. 28); this is the simplest way to diagnose the species. In occasional specimens the long spermathecal extensions are visible through the integument when the epigynum is examined ventrally (Fig. 16). In *W. subspiralis* the extension of the spermatheca is of similar type, but shorter (Figs. 29, 31), and the double spiral path has fewer turns (Figs. 26, 27). In *W. microspiralis* and *W. latens* the spermathecal extension and the duct spiral are even shorter (Figs. 30, 32; 41, 48), and the duct pathway after leaving the extension is somewhat shorter and simpler (Figs. 26, 41). *W. spiralis* female is readily distinguishable from *W. arctica* and *W. saniuana* (which are grouped with it in the key) by the form of the spermathecal extension.

Distribution.—*W. spiralis* is widely distributed throughout N. America (Map 1), but appears to be absent from the western coastal area, where it is replaced by *W. subspiralis*. The records mapped are based exclusively on females, since unaccompanied males cannot be distinguished from *W. subspiralis*, and possibly from *W. microspiralis*.

Natural History.—Adult females have been taken from March to November, males from May to October. The species has been taken in a variety of habitats: in meadows, in tall grass and weeds, in sphagnum fen, on beach dunes, at the edge of woods, and by beating bushes.

Walckenaeria subspiralis, new species

Figs. 24, 26, 27, 29, 31; Map 2

Type.—Holotype female from 9 mi. south-west of Tule Lake, Siskiyou Co., California, 15 September 1965 (J. and W. Ivie); deposited in AMNH.

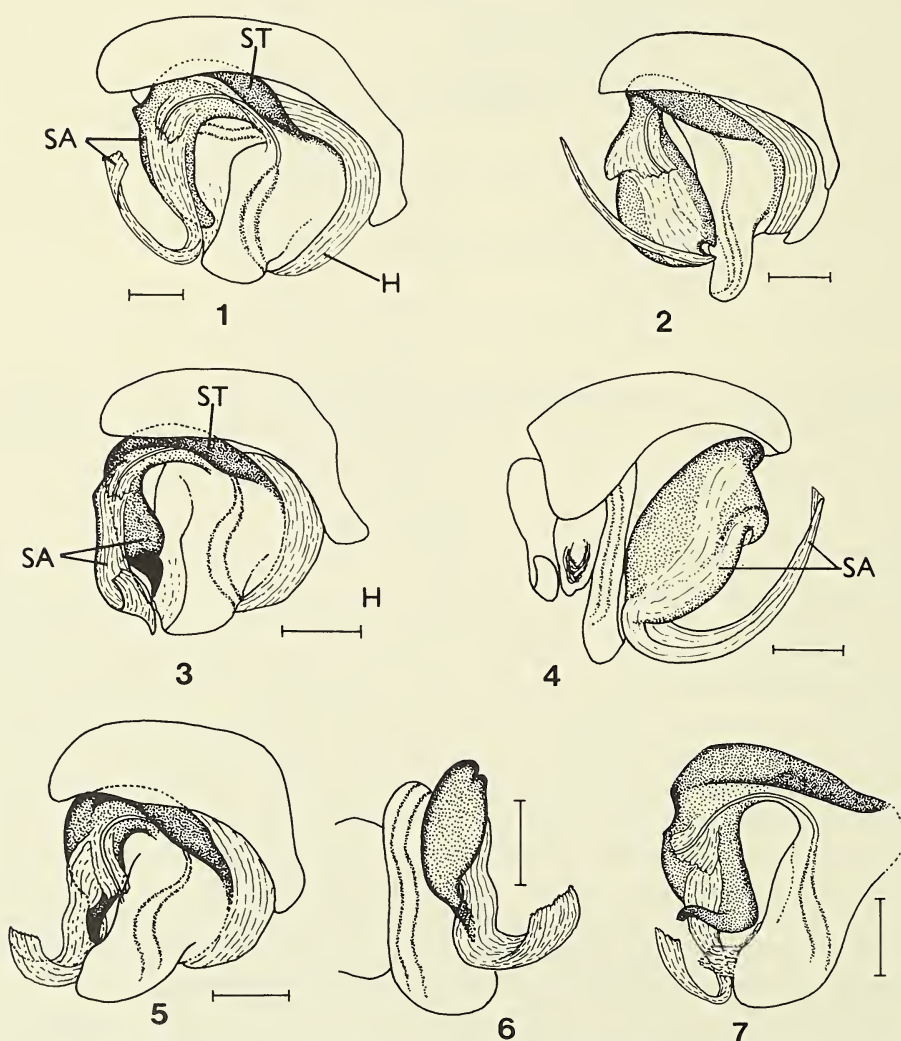
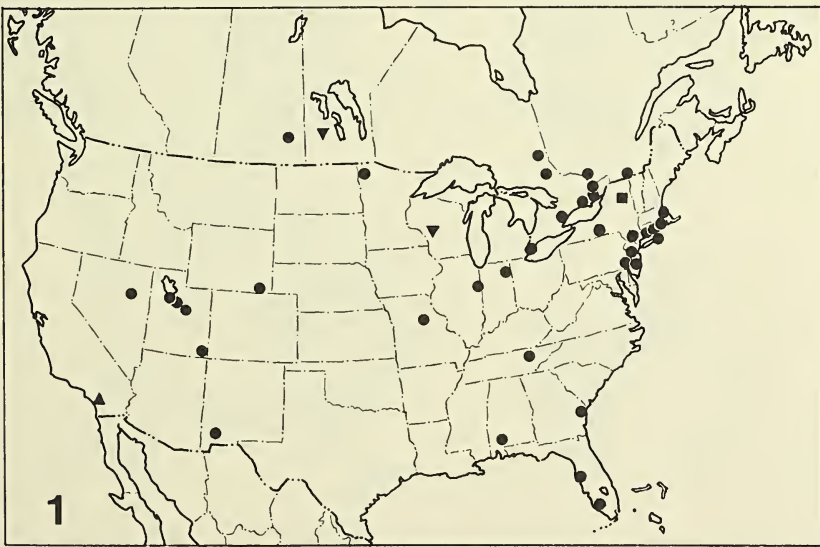


Fig. 1-7.—Male palpal organs, with ED removed, 1, *W. acuminata*, mesal; 2, *W. spiralis*, mesal; 3, *W. unicornis*, mesal; 4, *W. spiralis*, ectal; 5, *W. clavicornis*, mesal; 6, *W. clavicornis*, ectal; 7, *W. cuspidata*, mesal. Abbreviations: SA, suprategular apophysis; ST, suprategulum (Scale lines 0.1 mm).

Description.—Total length: female 2.1-2.9 mm, male 1.9-2.3 mm. Carapace: length: female 0.9-1.1 mm, male 0.9-1.0 mm. In color and most characters this species seems to be identical with *W. spiralis*. Male palp: not distinguishable from that of *W. spiralis*. Epigynum: externally not distinguishable from that of *W. spiralis*, except in occasional specimens where the form of the spermathecal extensions is visible through the integument. Internally the duct leaves the spermatheca via a double spiral of 2-3 turns in each direction (Fig. 26) inside the screw-like, dark colored extension (Figs. 29, 31); thereafter (Fig. 24) the duct follows a similar course to that in *W. spiralis*. In a few specimens, which are assumed to be of the same species, the wall of the spermathecal extension is much less evident, and after clearing is more or less invisible (Fig. 27).

Diagnosis.—The male of *W. subspiralis* is structurally indistinguishable from *W. spiralis*, and is distinguishable from *W. microspiralis* only by the value of TmI (see *W. spiralis* diagnosis). The epigynum of *W. subspiralis* is in most instances indistinguishable from that of *W. spiralis* and several other species, and the female must be diagnosed by the internal genitalia. The form of the squat beehive-shaped extension of the spermatheca (Figs. 29, 31) is distinctive: this is shorter than in *W. spiralis* (Fig. 28), and the double spiral pathway of the duct inside this extension is also shorter (Fig. 26 cf. Fig. 23), but longer than in *W. microspiralis* (Figs. 30, 32). The female can usually be diagnosed without difficulty in the same way as with *W. spiralis*, by lifting the epigynum and observing the dorsal side (Fig. 29). *W. subspiralis* female is readily distinguished from *W. arctica*, *W. saniuana* and *W. latens* (which are associated with it in the key) by the form of the spermathecal extension and of the double spiral pathway of the duct within the extension.

Distribution.—This species has been taken widely throughout N. America (Map 2: based on females), though there are more records from the west than from the east. The distribution appears somewhat discontinuous, but the structural differences between the eastern and western populations are too small to justify regarding these as separate species.



Map 1.—North America. Distributions of *W. spiralis* (circles), *W. saniuana* (triangle), *W. redneri* (inverted triangles) and *W. clavipalpe* (square).

Natural History.—Adult females have been taken from March to December, males from June to November. This species has been recorded from a variety of habitats: e.g. in grass, in leaf litter, in sphagnum, in cracks in dried mud, on a rocky lake shore, under logs, in a soil sample and by sweeping low vegetation.

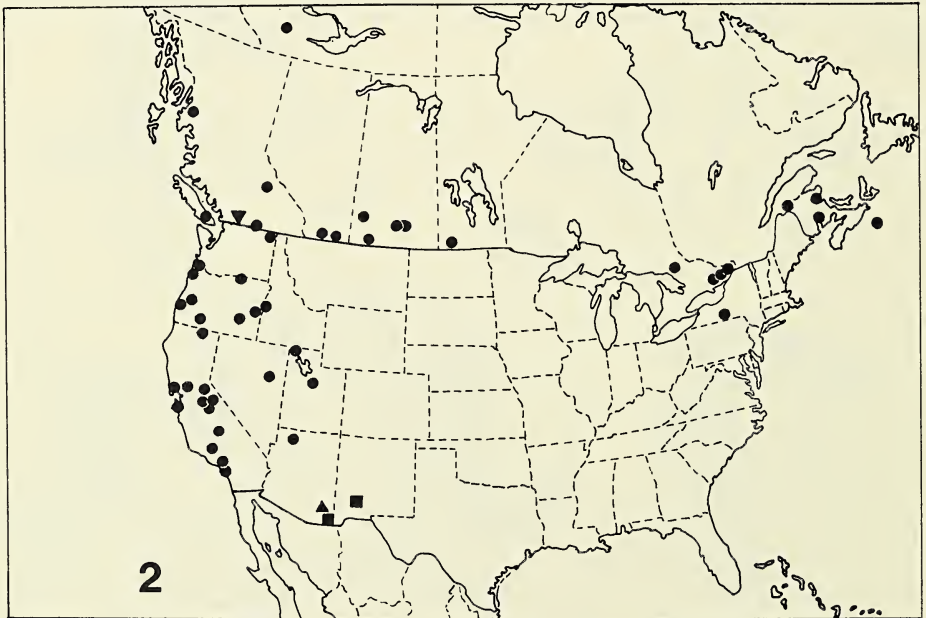
Walckenaeria microspiralis, new species

Figs. 17, 25, 30, 32, 110; Map 7

Type.—Holotype female from Richmond, Ontario, 12-27 July 1978, pitfalls in calcareous bog (Dondale and Redner); deposited in CNC.

Description.—The two sexes were taken together. Total length: female 3.1-3.3 mm, male 2.45 mm. This species is colored more or less the same as *W. spiralis*. Carapace: length: female 1.30-1.35 mm, male 1.0 mm. The male carapace is slightly raised behind the eyes (Fig. 110), but this character shows some variation. Legs: TmI: female 0.70-0.75, male 0.65. Chelicerae: in the female the lateral striae are more closely spaced than in *W. spiralis*, while in the male they are rather more widely spaced. Male palp: identical with that of *W. spiralis*. Epigynum: Fig. 17; externally the spermathecae appear very dark in color, but whether this is a constant character is uncertain. Internally, the duct leaves the spermatheca via a short double spiral of about one turn in each direction (Fig. 30) inside the squat, dark colored screw-like extension (Fig. 32)? thereafter the duct follows a shorter, rather more regular route (Fig. 25) than in *W. spiralis* or *W. subspiralis*.

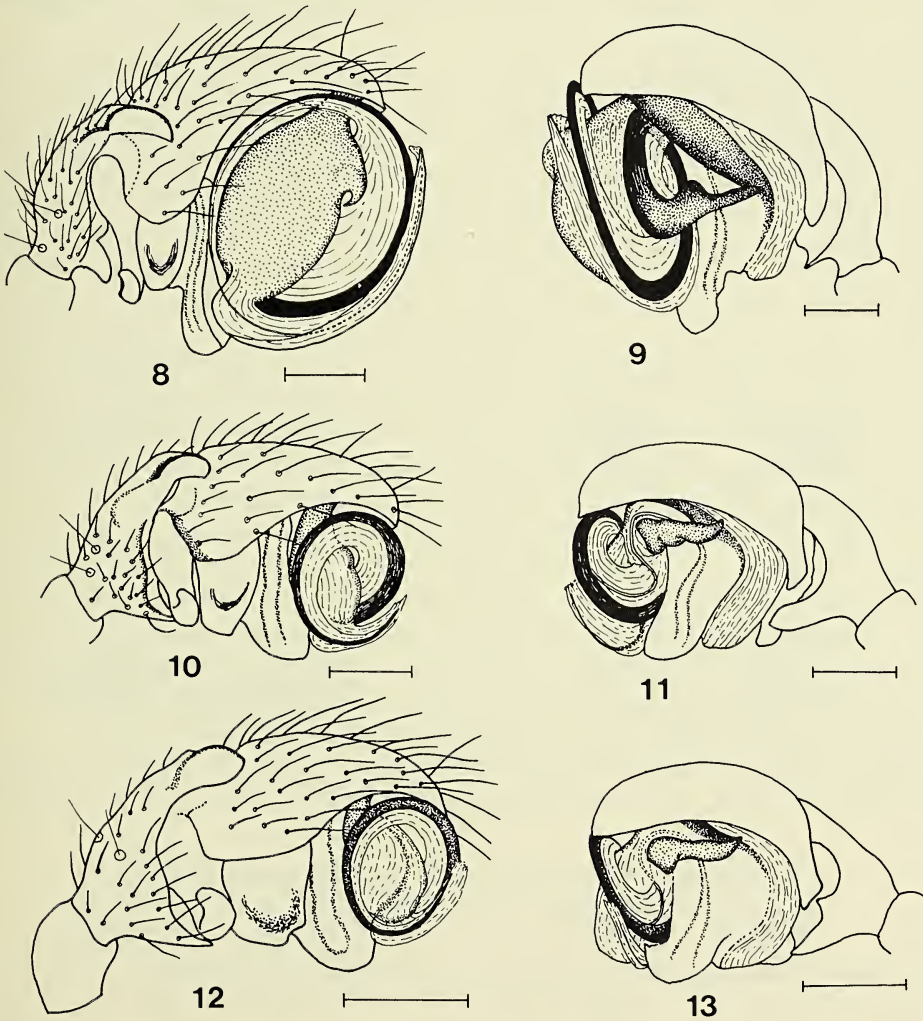
Diagnosis.—The male of *W. microspiralis* appears to be distinguishable from *W. spiralis* and *W. subspiralis* only by the higher value of TmI (0.65 cf. 0.50-0.55), though examination of more specimens may show that this difference is not always reliable. The female



Map 2.—North America. Distributions of *W. subspiralis* (circles), *W. latens* (triangle), *W. pallax* (inverted triangles) and *W. blanda* (squares).

can possibly be distinguished from *W. spiralis* and *W. subspiralis* by the epigynum (Fig. 17), but a more reliable diagnosis is based on the form of the spermathecal extension (Fig. 32), in which the duct follows a double spiral path of about one turn in each direction (Fig. 30). The epigynum and internal genitalia of *W. microspiralis* are similar to those of *W. latens* (Figs. 20, 41); the spermathecae in *W. latens* are differently shaped, however, and the pathway of the duct after leaving the spermathecal extension is longer and more complex in *W. microspiralis* than in *W. latens*. In addition, the value of TmI in *W. microspiralis* (0.70) is much higher than in *W. latens* (0.50), and the geographical distributions of the two species is different. *W. microspiralis* is readily distinguished from *W. saniuana* and *W. arctica* (which are associated with it in the key) by the form of the spermathecal extension (Fig. 32 cf. Fig. 46). *W. microspiralis* female is also rather similar to *W. pullata*: see *W. pullata* diagnosis.

Distribution.—This species is known only from a small area of the eastern part of N. America (Map 7: based on females).



Figs. 8-13.—Male palps. 8, *W. spiralis*, ectal; 9, *W. spiralis*, mesal; 10, *W. arctica*, ectal; 11, *W. arctica*, mesal; 12, *W. saniuana*, ectal; 13, *W. saniuana*, mesal (Scale lines 0.1 mm).

Natural History.—Females were taken adult in June to August, males in June-July. The species has been recorded from boggy areas, and on a beach.

Walckenaeria arctica, new species
Figs. 10, 11, 18, 39, 46, 68; Map 7

Type.—Holotype male from Wrigley, Northwest Territories, Canada, 6-12 June 1969 (G. E. Shewell); deposited in CNC.

Description.—The female described was taken at the type locality within a few days of the male. Total length: female 2.2-2.3 mm, male 1.80-1.85 mm. Carapace: length: female 0.90 mm, male 0.80 mm. Chestnut-brown, with margins darkened. Chelicerae: lateral striae less widely spaced in both sexes than in *W. spiralis*. Abdomen: grey to black. Sternum: orange brown to deep brown, with darkened margins. Legs: orange-brown to brown. TmI: female 0.46-0.50, male 0.44-0.48. Male palp: Figs. 10, 11, 68. Epigynum: Figs. 18, 39, 46.

Diagnosis.—*W. arctica* male is diagnosed by the palp (Figs. 10, 11), which has the embolic coil of medium size. The species with which confusion is most likely is *W. saniuana*; the notch on the anterior margin of the SA in *W. arctica* is more pronounced than in *W. saniuana* (Fig. 10 cf. Fig. 12), and the cheliceral striae are significantly more closely spaced in *W. arctica*. In addition, the palpal tibia of *W. arctica* has three trichobothria, whereas *W. saniuana* has only two (Fig. 68, cf. Fig. 69), and the geographical distributions of the two species are different. The female of *W. arctica* has the epigynum (Fig. 18) very similar to those of *W. spiralis* and several other species, and the diagnosis must be based on the internal genitalic structure (Figs. 39, 46). In *W. arctica*, the passage of the duct through the spermathecal extension is a smooth curve rather than a double spiral as is *W. spiralis*, *W. subspiralis*, *W. microspiralis* and *W. latens*. The epigynum and internal genitalia are very close to those of *W. saniuana* (Fig. 19) and *W. arcana* (Figs. 21, 40, 47). From these two species *W. arctica* is separated by the much closer spacing of the cheliceral striae; recourse must also be made to the geographical distribution, which for *W. arctica* is northern, and for *W. saniuana* and *W. arcana* is western and southern. Although the epigyna of *W. arctica* and *W. pullata* (Fig. 33) are probably distinguishable, the internal genitalia of these two species show fairly close similarities (Figs. 39, 42); the spermathecal extensions are however somewhat differently shaped (Fig. 46 cf. Fig. 49), and the duct pathway anterior to the spermatheca is more complex in *W. pullata*.

Distribution.—*W. arctica* is known only from a few localities in the north of the continent: New Hampshire, Alberta and Northwest Territories (Map 7).

Natural History.—Adult females have been taken in June and September, males in May-June and August. The only habitat recorded is in grass at the edge of a poplar wood.

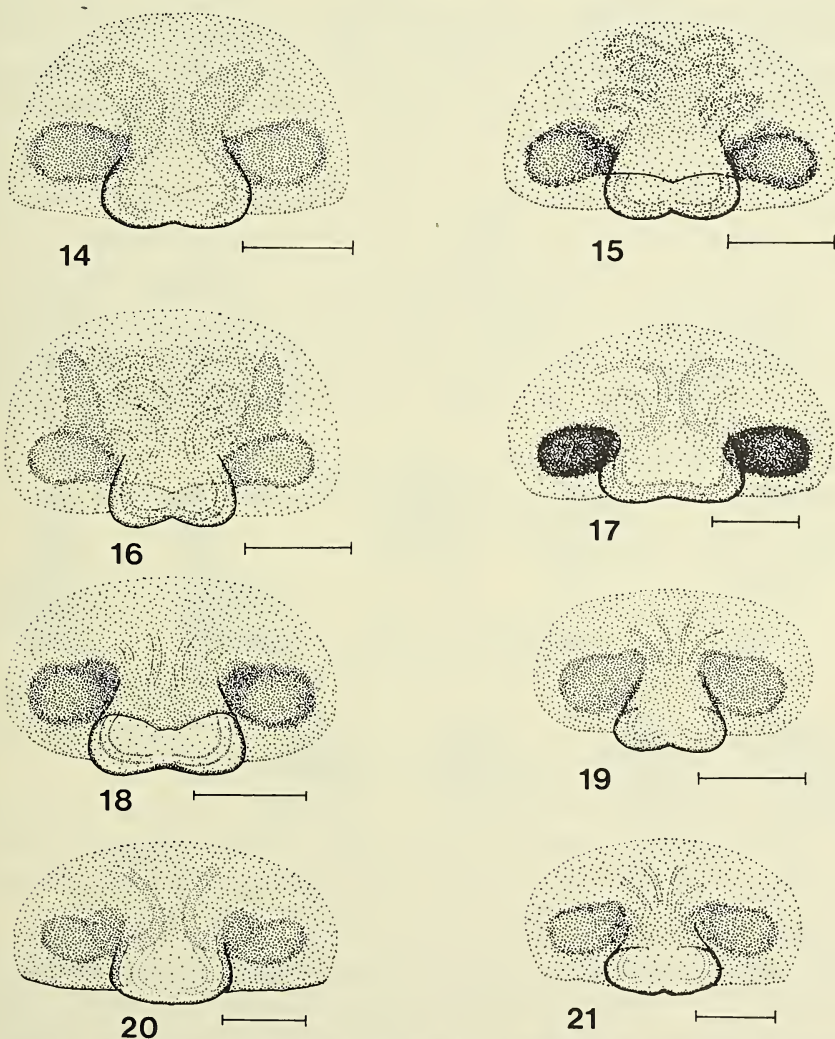
Walckenaeria saniuana (Chamberlin and Ivie), new combination
Figs. 12, 13, 19, 69; Map 1

Sisid saniuana Chamberlin and Ivie 1939:66; Roewer 1942:650; Bonnet 1958:4066.

Type.—Male type (labelled "Sisid A type") from San Juan Creek, Orange Co., California, 3 July 1931 (R. V. Chamberlin); in AMNH, examined. I have labelled this specimen as the holotype of *Sisid saniuana* Chamberlin and Ivie.

Description.—The female described was taken at the type locality two days before the type. Total length: female 2.0 mm, male 1.6 mm. Carapace: length: female 0.9 mm, male 0.7 mm. Brown, somewhat darkened anteriorly. Chelicerae: lateral striae widely separated in both sexes. Abdomen: grey-black. Sternum: brown, suffused with black. Legs: yellow-brown. TmI: female 0.53, male 0.50. Male palp: Figs. 12, 13, 69; the tibia has two trichobothria dorsally. Epigynum: Fig. 19: the internal genitalia are practically identical (apart from size) with those of *W. arcana* (Figs. 40, 47).

Diagnosis.—The male of *W. saniuana* is closely similar to *W. arctica*, and its diagnosis is dealt with under that species. The epigynum of *W. saniuana* (Fig. 19) is similar to those of other species in this group, and particularly to those of *W. arctica* (Fig. 18) and *W. arcana* (Fig. 21). From *W. arctica* it is separated by the much wider spacing of the cheliceral striae and the geographical distribution (see *W. arctica* diagnosis). From *W. arcana* it can be distinguished by the much larger size of the latter, by the proportions of



Figs. 14-21.—Epigyna. 14-16, *W. spiralis*; 17, *W. microspiralis*; 18, *W. arctica*; 19, *W. saniuana*; 20, *W. latens*; 21, *W. arcana* (Scale lines 0.1 mm).

the legs (MT I/tI 1.4, tibia I l/d ca. 4, cf. corresponding figs. of 1.7 and 5 for *W. arcana*), and possibly by the geographical distribution.

Distribution.—Known only from the type locality (Map 1).

Natural History.—Both sexes were adult in July; nothing was recorded on habitat.

Walckenaeria latens, new species

Figs. 20, 41, 48; Map 2

Type.—Holotype female from Heliograph Peak, Pinaleno Mts., Graham Co., Arizona, 29 August 1951 (T. Cohn); deposited in AMNH.

Description.—Only the female is known. Total length: female 3.3 mm. Carapace: length: female 1.2 mm. Chestnut-brown, with darker markings and margins. Chelicerae: lateral striae moderately widely spaced. Abdomen: black. Sternum: brown, reticulated with black. Legs: orange. TmI: female 0.50. Epigynum: Figs. 20, 41, 48.

Diagnosis.—The epigynum of *W. latens* (Fig. 20) is very similar to those of *W. spiralis* and several other species; consequently diagnosis must be based on the internal genitalia. The extension of the spermatheca (Fig. 48) and the short spiral pathway of the duct within the extension (Fig. 41) are very like those of *W. microspiralis* (Figs. 25, 30); for the distinguishing characters, see *W. microspiralis* diagnosis. *W. latens* is distinguished from *W. arctica* and *W. saniuana* (which are associated with it in the key) by the internal genitalia (see *W. arctica* diagnosis). The epigynum of *W. latens* is similar to that of *W. arcana* (Fig. 21); these two species are distinguished by the different forms of the spermathecal extension (Fig. 48 cf. Fig. 47), and by the spiral route of the duct in the extension in *W. latens* (Fig. 41, cf. Fig. 40). *W. latens* also has slimmer legs than *W. arcana*, with tibia I l/d 7.5-8 in *W. latens*, 5 in *W. arcana*, and the geographical distributions of the two species is probably different.

Distribution.—Known only by the type specimen (Map 2).

Natural History.—The single female was adult in August. Nothing was recorded on habitat, but possibly it is a montane species.

Walckenaeria arcana, new species

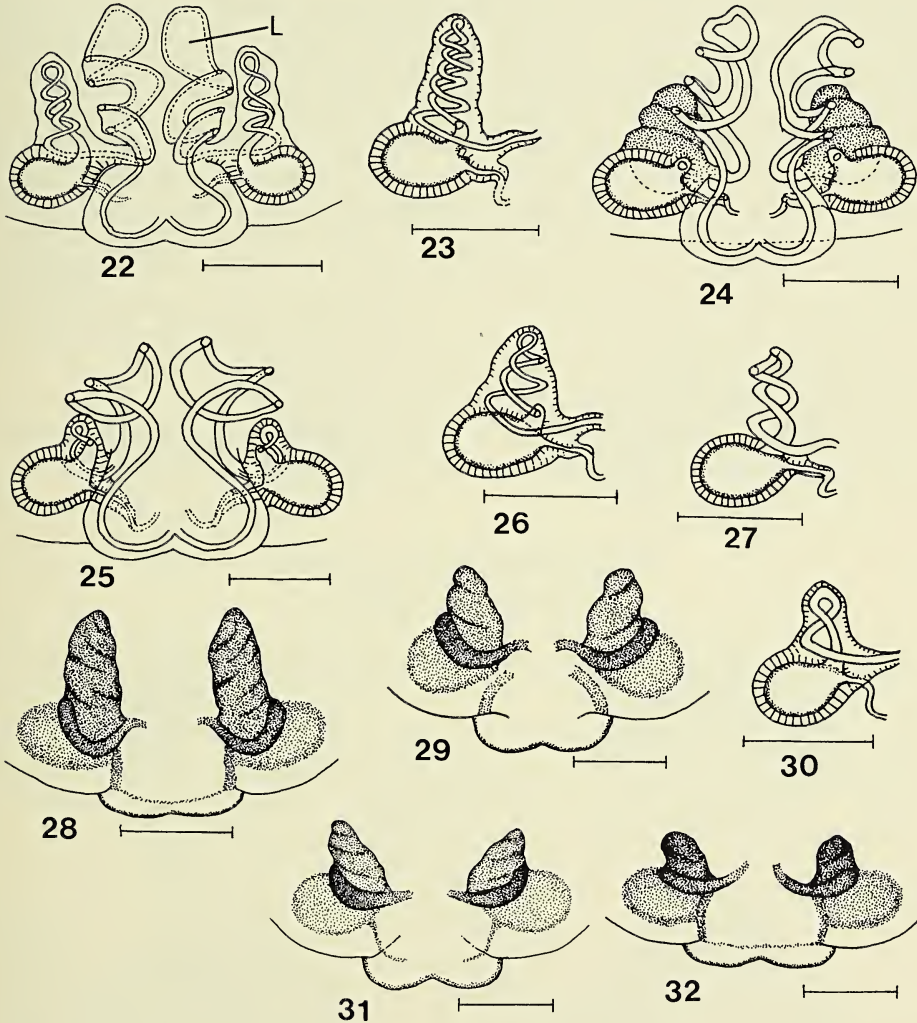
Figs. 21, 40, 47; Map 5

Type.—Holotype female from Laguna de Labradores, Galeana, Nuevo Leon, Mexico, 18 July 1942 (Bolivar, Bonet, Osorio, Pelaez); deposited in AMNH.

Description.—Only the female is known. Total length: female 3.3 mm. Carapace: length: female 1.2 mm. Orange-brown with dusky markings. Chelicerae: lateral striae widely spaced. Abdomen: grey. Sternum: orange, suffused with black, particularly on margins. Legs: orange. TmI: female 0.53-0.57. Epigynum: Figs. 21, 40, 47.

Diagnosis.—The epigynum of *W. arcana* (Fig. 21) is very similar to those of *W. spiralis* and its siblings, and particularly to those of *W. arctica* (Fig. 18), *W. saniuana* (Fig. 19) and *W. latens* (Fig. 20). Internally, the spermathecal extension and the ducts (Figs. 40, 47) are clearly distinct from those of *W. spiralis*, *W. subspiralis* and *W. microspiralis*, with the duct pathway within the extension following a smooth curve rather than a spiral. The internal genitalia are very similar to those of *W. arctica* (Figs. 39, 46); the separation of

these two species is based on the cheliceral striae and the geographical distribution (see *W. arctica* diagnosis). *W. arcana* is larger in size than *W. saniuana*, but otherwise very similar: for distinguishing characters, see *W. saniuana* diagnosis. The epigynum of *W. arcana* is also similar to that of *W. latens* (Fig. 20): the distinguishing characters are given under *W. latens* diagnosis. Although the epigyna of *W. arcana* and *W. pullata* (Fig. 33) are probably distinguishable their internal genitalia are rather similar (Figs. 40, 42); the spermathecal extensions are however rather differently shaped (Fig. 47 cf. Fig. 49), and the duct pathway after leaving the extension is more complex in *W. pullata*. See also *W. discolor* and *W. faceta* diagnoses.



Figs. 22-32.—Female genitalia, internal. 22, *W. spiralis*, cleared, ventral; 23, *W. spiralis*, spermatheca, cleared, dorsal; 24, *W. subspiralis*, cleared, dorsal; 25, *W. microspiralis*, cleared, dorsal; 26, *W. subspiralis*, spermathecae, cleared, dorsal; 27, *W. subspiralis*, spermathecae, cleared, dorsal, another specimen (see text); 28, *W. spiralis*, spermathecae, dorsal; 29, *W. subspiralis*, spermathecae, dorsal; 30, *W. microspiralis*, spermathecae, cleared, dorsal; 31, *W. subspiralis*, spermathecae, dorsal, specimen from California; 32, *W. microspiralis*, spermathecae, dorsal. Abbreviation: L, lamella carrying ducts (Scale lines 0.1 mm).

Distribution.—Known only from the type locality in Mexico (Map 5).

Natural History.—The single female was taken adult in July; nothing was recorded on habitat.

Walckenaeria pullata, new species

Figs. 33, 42, 49; Map 11

Type.—Holotype female from Mirror Lake, Uintah Mts., Duchesne Co., Utah, 22 September 1932 (W. Ivie); deposited in AMNH.

Description.—Only the female is known. Total length: female 2.55-2.65 mm. Carapace: length: female 1.0 mm. Deep orange, heavily suffused with chestnut or black. Chelicerae: lateral striae widely spaced. Abdomen: black. Sternum: deep chestnut brown. Legs: deep orange. TmI: female 0.48-0.51. Epigynum: Figs. 33, 42, 49.

Diagnosis.—*W. pullata* can probably be diagnosed by the epigynum (Fig. 33), though this is rather similar to that of *W. microspiralis* (Fig. 17). The identification should always be checked by examination of the internal genitalia; the form of the spermathecal extension (Fig. 49) and the non-spiral pathway of the duct within the extension (Fig. 42) distinguish *W. pullata* from *W. microspiralis* (Figs. 32, 30). The value of TmI for *W. pullata* (0.50) is also much lower than for *W. microspiralis* (0.70). The internal genitalia of *W. pullata* have a similar form to those of *W. arctica* (Fig. 39) and *W. arcana* (Fig. 40): for distinguishing characters, see *W. arctica* and *W. arcana* diagnoses.

Distribution.—Known only from Utah and Alberta (Map 11).

Natural History.—Females were adult in August and September. The habitat recorded in Alberta was in pine litter/red heath mat on an alpine slope at ca. 2000 m.

Walckenaeria discolor, new species

Figs. 34, 43, 50; Map 3

Type.—Female holotype from 2 mi. east of El Salto, Durango, Mexico, 10 July 1964 (E. E. Linquist); deposited in CNC.



Map 3.—Mexico. Distribution of *W. discolor* (circles), *W. iviei* (triangle), *W. faceta* (inverted triangle) and *W. rufula* (square).

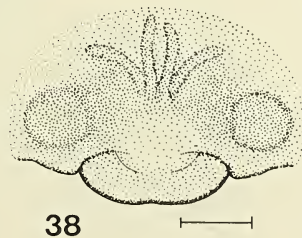
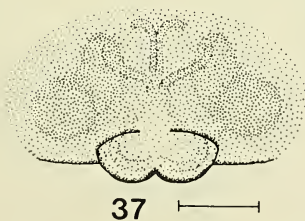
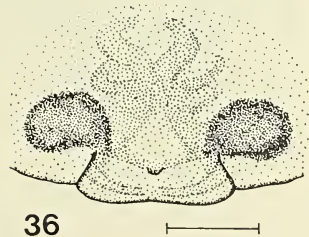
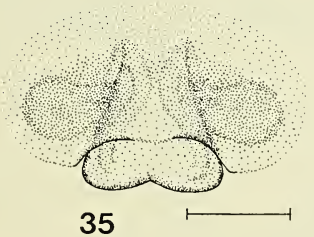
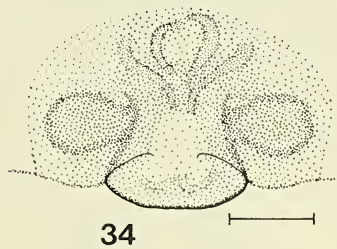
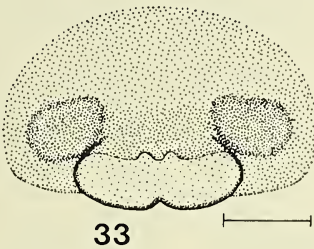
Map 4.—Mexico. Distributions of *W. crocea* (circle), *W. gertschi* (triangles), *W. rutilis* (inverted triangles) and *W. aenea* (square).

Description.—Only the female is known. Total length: female: 2.55-3.10 mm. Carapace: length: female 1.05-1.10 mm. Orange-brown, with faint darker markings. Chelicerae: lateral striae moderately spaced. Abdomen: grey-black, with four pale chevrons dorsally, and a longitudinal white stripe ventrally. Sternum: pale orange, with dusky markings. Legs: orange-brown. TmI: female 0.57. Epigynum: Figs. 34, 43, 50; the ducts are clearly visible anteriorly.

Diagnosis.—The epigynum of *W. discolor* is generally similar to those of *W. iviei* (Fig. 37), *W. rutilis* (Fig. 38), *W. faceta* (Fig. 36) and *W. arcana* (Fig. 21), all of which have a similar geographical distribution to *W. discolor*. The coloration will distinguish *W. discolor* from *W. iviei* and *W. rutilis*, but separation from *W. faceta* and *W. arcana* must be based on the internal genitalia. In *W. discolor* the extension of the spermatheca is distinctly more curved than in *W. faceta* or *W. arcana* (Fig. 43, 50, cf Figs. 44, 51; 40, 47) and the arrangement of the ducts after leaving the extension is simpler than in *W. faceta*. The internal genitalia also serve to prevent any confusion of *W. discolor* with *W. spiralis* and its siblings. The presence in *W. discolor* of the pale colored abdominal chevrons and ventral stripe are confirmatory characters in diagnosis.

Distribution.—Known only from one area in Mexico (Map 3).

Natural History.—Both the known females were adult in July. One habitat recorded was pine duff.



Figs. 33-38.—Epigyna. 33, *W. pullata*; 34, *W. discolor*; 35, *W. blanda*; 36, *W. faceta*; 37, *W. iviei*; 38, *W. rutilis* (Scale lines 0.1 mm).

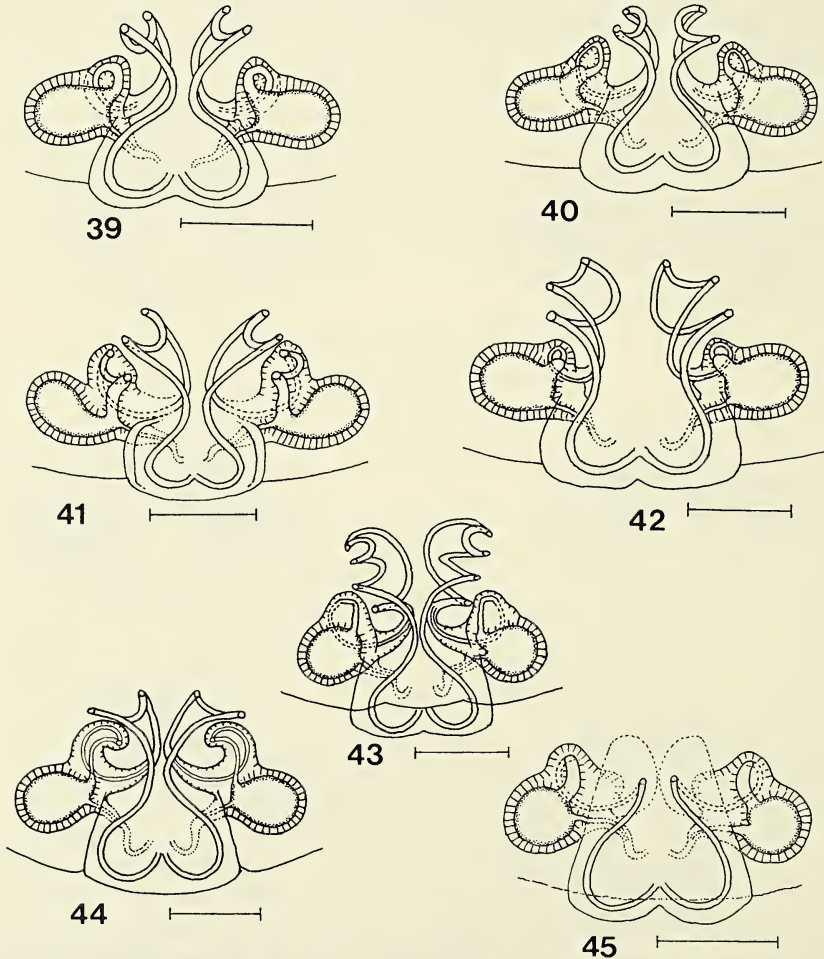
Walckenaeria faceta, new species

Figs. 36, 44, 51; Map 3

Type.—Female holotype from Volcan Tzontehuitz (altitude 3000 m), 12 mi. N.E. of San Cristobal de las Casas, Chiapas, Mexico, 27 May 1964 (W. M. Campbell); deposited in CNC.

Description.—Only the female is known. Total length: female 2.65 mm. Carapace: length: female 1.1 mm. Brown to dark brown. Chelicerae: lateral striae fairly widely spaced. Abdomen: grey. Sternum: brown. Legs: brown. TmI: female 0.58-0.62. Epigynum: Figs. 36, 44, 51.

Diagnosis.—The epigynum of *W. faceta* (Fig. 36) is generally similar to those of *W. iviei* (Fig. 37), *W. rutilis* (Fig. 38), *W. discolor* (Fig. 34) and *W. arcana* (Fig. 21), all of which have a similar distribution to *W. faceta*. The coloration will distinguish *W. faceta* from *W. iviei* and *W. rutilis*, but separation from *W. discolor* and *W. arcana* is best based on the internal genitalic structure. The principal difference from *W. arcana* lies in the more complicated duct pathway present in *W. faceta* (Fig. 44 cf. Fig. 40); the legs of *W.*



Figs. 39-45.—Female genitalia, cleared, dorsal. 39, *W. arctica*; 40, *W. arcana*; 41, *W. latens*; 42, *W. pullata*; 43, *W. discolor*; 44, *W. faceta*; 45, *W. blanda* (Scale lines 0.1 mm).

faceta are also somewhat stouter, with tibia I l/d 3.5-4 cf. ca. 5 for *W. arcana*. The separation from *W. discolor* is dealt with under that species. The internal genitalia of *W. faceta* also serve to prevent any confusion with *W. spiralis* and its siblings.

Distribution.—Known only from the type locality, where it has been taken on two separate occasions.

Natural History.—The females were adult in May. Habitats recorded were in deciduous leaf litter, and in moss from a log.

Walckenaeria pallax, new species

Figs. 55, 56; Map 2

Type.—Male holotype from Manning Provincial Park, British Columbia, 19 June-4 July 1979 (C. D. Dondale); deposited in CNC.

Description.—Only the male is known. Total length: male 2.3 mm. Carapace: length: male 0.95 mm. Brown, with dusky markings, and with a black blotch on the clypeus below the anterior median eyes. Chelicerae: lateral striae more narrowly spaced than in *W. spiralis*. Abdomen: grey-black. Sternum: brown, suffused with black, particularly on margins. Legs: orange. TmI: male 0.47. Male palp: Figs. 55, 56; the embolic coil is large. The palpal tibia is identical with that of *W. spiralis* (Fig. 67).

Diagnosis.—*W. pallax* is diagnosed by the male palp (Fig. 55), which has the embolic coil larger than that of any species except *W. spiralis* and its siblings; the tegulum is less extended ventrally in *W. pallax* than in *W. spiralis* (Fig. 8), and the small projection on the anterior margin of the SA is less hook-shaped. The tailpiece of *W. pallax* is quite distinct from that of *W. spiralis* (Fig. 56 cf. Fig. 9). *W. pallax* differs from *W. fallax* and *W. subvigilax* by the larger embolic coil (Fig. 55 cf. Figs. 57, 59), and by the shape of the tailpiece (Fig. 56, cf. Figs. 58, 60); the value of TmI is also much lower in *W. pallax* (0.47) than in *W. fallax* (0.65-0.70).

Distribution.—Known only from the type locality (Map 2).

Natural History.—The male was taken adult in June-July, in a pitfall at the edge of a pond.



Map 5.—Mexico and Texas. Distribution of *W. mexicana* (circle), *W. puella* (triangle), *W. aurata* (inverted triangle) and *W. arcana* (square).

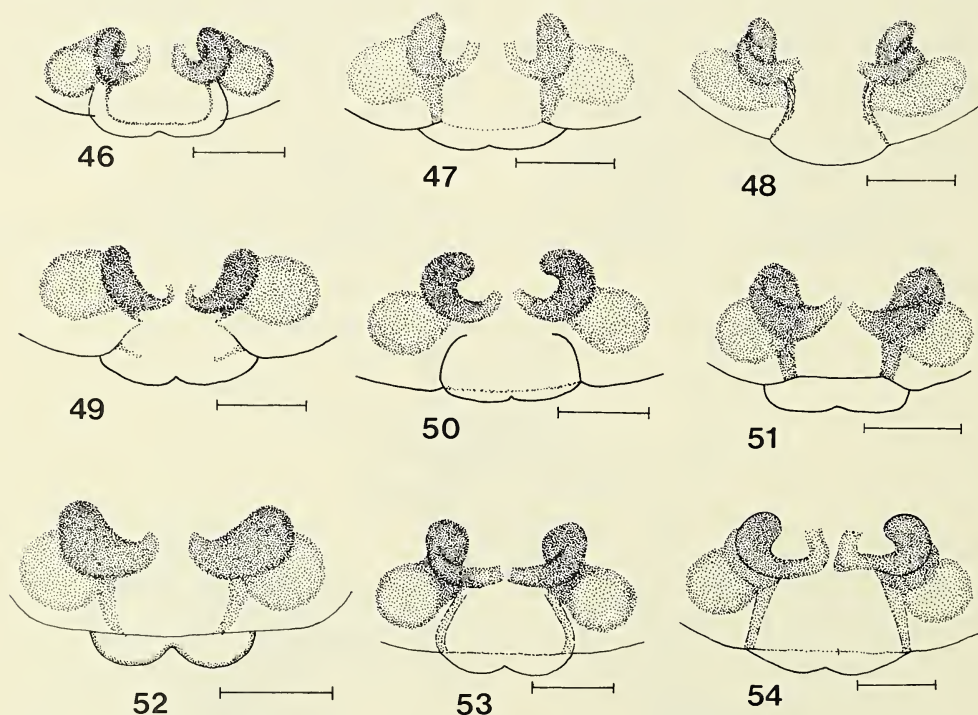
Walckenaeria fallax, new species

Figs. 57, 58, 71; Map 7

Type.—Male holotype from Poltimore, Quebec, 13 June-5 July 1979 (J. H. Redner); deposited in CNC.

Description.—Only the male is known. Total length: male 2.3-2.45 mm. Carapace: length: male 1.1-1.15 mm. Deep brown, suffused with black anteriorly. Chelicerae: lateral striae fairly closely spaced, much closer than in *W. spiralis*. Abdomen: black. Sternum: brown, with black markings and margins. Legs: brown to deep brown. TmI: male 0.65-0.70. Male palp: Figs. 57, 58, 71; the embolic coil is fairly large. The palpal tibia (Fig. 71) is somewhat different from that of *W. spiralis*.

Diagnosis.—*W. fallax* is diagnosed by the male palp (Fig. 57), which has the embolic coil moderately large, but noticeably smaller than those of *W. spiralis* (Fig. 8) or *W. pella* (Fig. 55); the tailpiece (Fig. 58) is similar to that of *W. spiralis* (Fig. 9). The only species which have the embolic coil similar in size are *W. subvigilax* (Fig. 59), the European species *W. vigilax* (Fig. 125) and the Mexican species *W. rutilis*. Confusion with *W. rutilis* is impossible because of its much brighter orange color; the tibial apophyses are also rather different in shape (Fig. 71 cf. Fig. 83). *W. subvigilax* and *W. vigilax* lack the small projection present on the anterior margin of the SA in *W. fallax*, and the tailpiece of *W. fallax* (Fig. 58) differs from those of *W. subvigilax* (Fig. 60) and *W. vigilax* (Fig. 126). Additional differences are that *W. fallax* has the cheliceral striae more closely spaced, and a higher value for TmI (0.65-0.70, cf. 0.52 for *W. subvigilax* and 0.50-0.55 for *W. vigilax*).



Figs. 46-54.—Female genitalia, spermathecae, dorsal. 46, *W. arctica*; 47, *W. arcana*; 48, *W. latens*; 49, *W. pullata*; 50, *W. discolor*; 51, *W. faceta*; 52, *W. blanda*; 53, *W. iviei*; 54, *W. rutilis* (Scale lines 0.1 mm).

Distribution.—This species has been taken only in Canada (Quebec, Ontario and Alberta) (Map 7).

Natural History.—Males were adult in June–August. Habitats recorded are in sphagnum, in calcareous bogs and at the edge of deciduous woods (pitfall).

Walckenaeria subvigilax, new species

Figs. 59, 60, 70; Map 11

Type.—Male holotype from Canyon east of Bedford, Lincoln Co., Wyoming, 27 June 1962 (W. Ivie); deposited in AMNH.

Description.—Only the male is known. Total length: male 2.10 mm. Carapace: length: male 0.95 mm. Deep chestnut brown. Chelicerae: lateral striae moderately widely separated. Abdomen: black. Sternum: orange, suffused with black. Legs: orange, with patellae paler. TmI: male 0.52. Male palp: Figs. 59, 60, 70. It is possible, based on geographical distributions, that this is the male of *W. pullata* or *W. latens*.

Diagnosis.—*W. subvigilax* is diagnosed by the male palp (Fig. 59), which has the embolic coil moderately large, more or less as in *W. fallax* (Fig. 57): for the characters distinguishing these two species, see *W. fallax* diagnosis. The Mexican species *W. rutilis*, which has the embolic coil rather similar in size, is distinguished by its much brighter color and by the somewhat different shape of the tibial apophysis (Fig. 83 cf. Fig. 70). *W. subvigilax* is very similar to the European species *W. vigilax* (Fig. 59 cf. Fig. 125), but the tailpiece is longer (Fig. 60 cf. Fig. 126), the embolic coil is slightly larger and the color is more brightly orange.

Distribution.—Known only from the type locality (Map 11).

Natural History.—The male was adult in June: nothing was recorded on habitat.

Walckenaeria iviei, new species

Figs. 37, 53, 61, 62, 80, 102; Map 3

This species is named in honor of W. Ivie, who was responsible for the capture of several new *Walckenaeria* species.

Type.—Male holotype from Garnica Pass summit (9,300 ft.), Mexico, 8 May 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 2.90 mm, male 2.1–2.3 mm. Carapace: length: female 1.15 mm, male 0.95 mm. Bright orange, with ocular area suffused with black and eyes circled with black. Chelicerae: lateral striae moderately spaced in both sexes. Abdomen: greyish white. Sternum: orange. Legs: femora bright orange, remaining segments yellow-brown to deep brown. TmI: female 0.53, male 0.50. Male palp: Figs. 61, 62, 80; orange, with tibial apophysis deep brown distally. Epigynum: Figs. 37, 53, 102.

Diagnosis.—*W. iviei* can be diagnosed in the male by its bright color, by the form of the palp (Figs. 61, 62, 80) and by its geographical distribution. It is very similar to *W. rutilis* and *W. crocea*, from which *W. iviei* differs chiefly by the smaller diameter of its embolic coil (Fig. 61, cf. Figs. 63, 74). The female of *W. iviei* is diagnosed by its color and by the characteristic epigynum (Fig. 37), which in the only female I have seen is distinguishable from that of the closely related *W. rutilis* (Fig. 38) by the form of the internal ducts

which are visible through the integument. *W. iviei* and *W. rutilis* are readily separable by their internal genitalia, the ducts being shorter with a differently shaped path in *W. iviei* (Fig. 102, cf. Fig. 103), and the spermathecal extensions being differently shaped (Fig. 53, cf. Fig. 54).

Distribution.—Known only from the type locality in Mexico (Map 3).

Natural History.—Both sexes were adult in May; nothing was recorded on habitat.

Walckenaeria rutilis, new species

Figs. 38, 54, 63, 64, 83, 103; Map 4

Type.—Male holotype from 2 miles S.W. of Rio Frio, Puebla, Mexico, 2 May 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 2.4-3.0 mm, male 2.1 mm. Carapace: length: female 1.0-1.15 mm, male 1.0 mm. Bright orange, with the eyes circled with black. Chelicerae: lateral striae moderately spaced in female, fairly widely spaced in male. Abdomen: whitish grey. Sternum: yellow to orange. Legs: femora orange, with the remaining segments a contrasting chestnut brown. TmI: female 0.45-0.50, male 0.51. Male palp: Figs. 63, 64, 83; orange, with the tibial apophysis deep brown distally. Epigynum: Figs. 38, 54, 103.

Diagnosis.—*W. rutilis* is diagnosed in the male by its bright coloration, by the form of the palp (Fig. 63), and by its geographical distribution. This species is distinguished from *W. iviei* male by the larger diameter of the embolic coil (Fig. 63, cf. Fig. 61). The palp of *W. crocea* is closely similar to that of *W. rutilis*: for the distinguishing characters, see *W. crocea* diagnosis. The palp of *W. rutilis* is structurally similar to that of *W. subvigilax*, but the brighter color of *W. rutilis* and its geographical distribution are sufficient to separate these two species. The female of *W. rutilis* is diagnosed by its color and by its characteristic epigynum (Fig. 38), which may possibly not always be distinguishable from that of *W. iviei* (Fig. 37); these two species are however separable by the form of the internal ducts (Fig. 103 cf. Fig. 102).

Distribution.—Known only from two localities in Mexico (Map 4).

Natural History.—The female was adult in April, the male in April-May; nothing was recorded on habitat.

Walckenaeria rufula, new species

Figs. 65, 66, 84; Map 3

Type.—Male holotype from 2 miles S.W. of Rio Frio, Puebla, Mexico, 24 July 1956 (W. J. Gertsch and V. Roth); deposited in AMNH.

Description.—Only the male is known. Total length: male 1.90 mm. Carapace: length: male 0.85 mm. Orange, with dusky markings. Chelicerae: lateral striae moderately spaced. Abdomen: black. Sternum: pale orange. Legs: femora orange, the remaining segments brown. TmI: male 0.45. Male palp: Figs. 65, 66, 84; the embolic coil is relatively small in diameter.

Diagnosis.—*W. rufula* male is diagnosed by the male palp (Fig. 65), coupled with its relatively bright color and geographical distribution. The palp is generally similar to that of *W. iviei* (Fig. 61), but the palp itself and the embolic coil are significantly smaller; the tibia of *W. rufula*, viewed laterally, is more turned down distally (Fig. 65 cf. Fig. 61), and the tailpiece is shorter and different in form (Fig. 66 cf. Fig. 62).

Distribution.—Known only from the type locality in Mexico (Map 3).

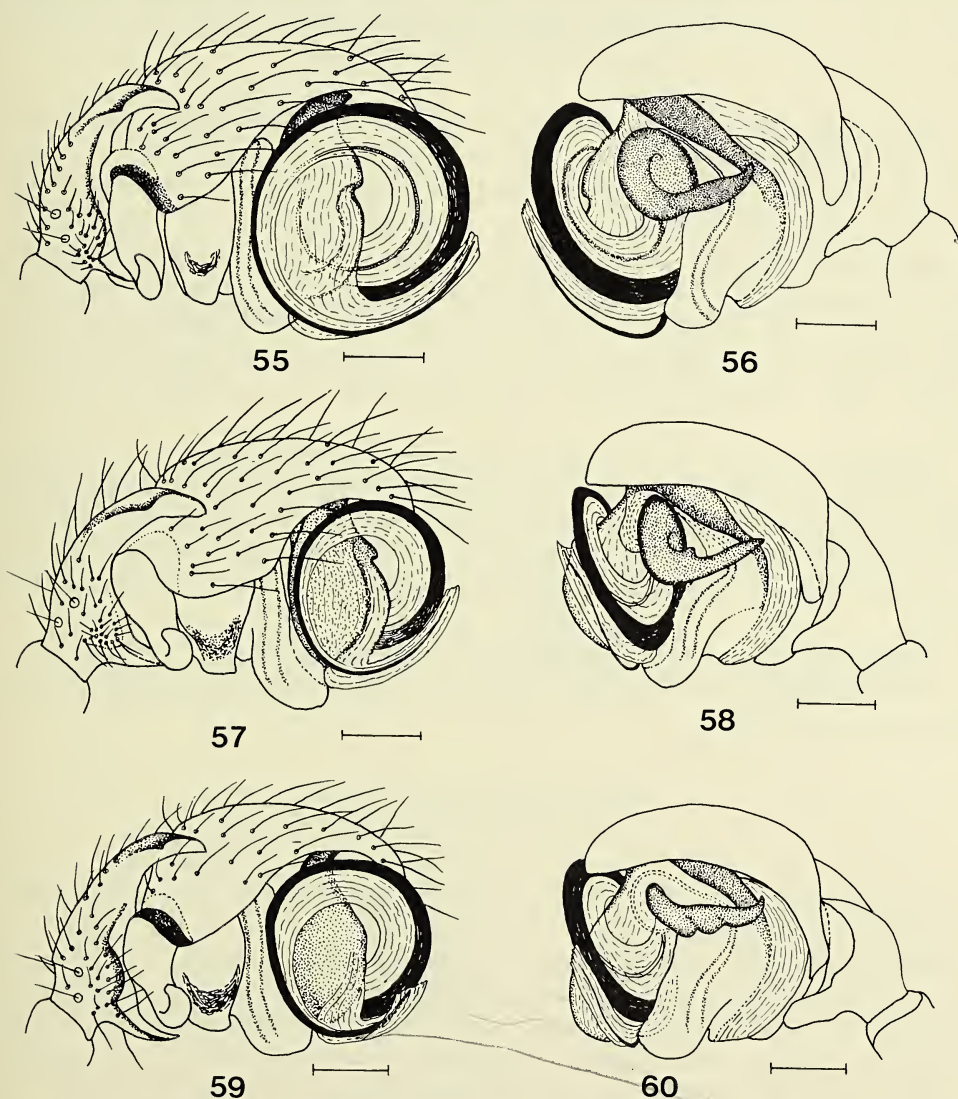
Natural History.—The male was adult in July: nothing was recorded on habitat.

Walckenaeria crocea, new species

Figs. 74, 75, 85, 86; Map 4

Type.—Male holotype from Tepetates Pass (15 miles W. Hidalgo), Michoacan, Mexico, 8 May 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Only the male is known. Total length: male 2.25 mm. Carapace: length: male 1.0 mm. Bright orange, with eyes circled with black. Chelicerae: lateral striae moderately spaced. Abdomen: almost white. Sternum: orange. Legs: femora bright



Figs. 55-60.—Male palps. 55, *W. pellax*, ectal; 56, *W. pellax*, mesal; 57, *W. fallax*, ectal; 58, *W. fallax*, mesal; 59, *W. subvigilax*, ectal; 60, *W. subvigilax*, mesal (Scale lines 0.1 mm).

orange, remaining segments chestnut brown. TmI: male 0.48. Male palp: Figs. 74, 75, 85, 86.

Diagnosis.—*W. crocea* male is diagnosed by the male palp (Fig. 74), by its bright coloration and by its geographical distribution. The palp is closely similar to that of *W. rutilis* (Fig. 63), but differs in the form of the SA, which has a membranous piece within the embolic coil (M, Figs. 74, 75) which is absent in *W. rutilis*; the inner margin of the embolic coil is not blackened as in *W. rutilis*, and the coil is slightly smaller. The palpal tibiae of these two species also show differences (Fig. 85 cf. Fig. 83), as do the tailpieces (Fig. 75 cf. Fig. 64).

Distribution.—Known only from the type locality, in Mexico (Map 4).

Natural History.—Two males were adult in May: nothing was recorded on habitat.

Walckenaeria gertschi, new species

Figs. 76, 81, 91, 106, 116; Map 4

This species is named in honor of Willis J. Gertsch, who has been responsible for the capture of several new *Walckenaeria* species.

Type.—Male holotype from Penuela, Veracruz, Mexico, 26 April 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—The two sexes were taken together. Total length: female 2.0-2.1 mm, male 1.65 mm. Carapace: length: female 0.95-1.0 mm, male 0.80 mm. Bright orange; the eyes are large (Fig. 116). Chelicerae: lateral striae fairly widely spaced in both sexes. Abdomen: grey-white. Sternum: yellow to orange, with dusky markings. Legs: yellow to orange. TmI: female/male 0.50-0.52. Male palp: Figs. 76, 81. Epigynum: Figs. 91, 106.

Diagnosis.—The male of *W. gertschi* is diagnosed by its coloration, by the form of the palp (Fig. 76) and particularly of the palpal tibia (Figs. 76, 81), and by its geographical distribution. No other known *Walckenaeria* species has the palpal tibia of this form. The female has a characteristic epigynum (Fig. 91), which distinguishes this species from all others. The diagnosis can be confirmed by the large eyes present in both sexes (Fig. 116).

Distribution.—Known only from two localities in Mexico (Map 4).

Natural History.—The female was adult in April, the males in April and May. Nothing was recorded on habitat.

Walckenaeria aenea, new species

Figs. 77, 82, 92, 104; Map 4

Type.—Male holotype from Tenejapa, Chiapas, Mexico, 22 July 1950 (C. Goodnight); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female: 2.55 mm, male 2.0-2.2 mm. Carapace: length: female 1.05 mm, male 0.95-1.0 mm. Bright orange, suffused with some brown. Chelicerae: lateral striae fairly widely spaced in both sexes. Abdomen: greyish white. Sternum: orange-yellow to orange-brown. Legs: brown to orange-brown. TmI: female/male 0.53. Tibial spines in both sexes 1111. Male palp: Figs. 77, 82. Epigynum: Figs. 92, 106.

Diagnosis.—The male of *W. aenea* is diagnosed by the form of the palp and of the palpal tibia (Figs. 77, 82), by its coloration and by its geographical distribution. No other

known species has the palpal tibia of the form shown. The female has a characteristic epigynum (Figs. 92, 106), which cannot be mistaken for that of any other species.

Distribution.—Known only from the type locality in Mexico (Map 4).

Natural History.—Both sexes were adult in July; nothing was recorded on habitat.

Walckenaeria capito (Westring)

Figs. 93, 97, 98, 99, 100, 101; Map 7

Erigone capito Westring 1861:213.

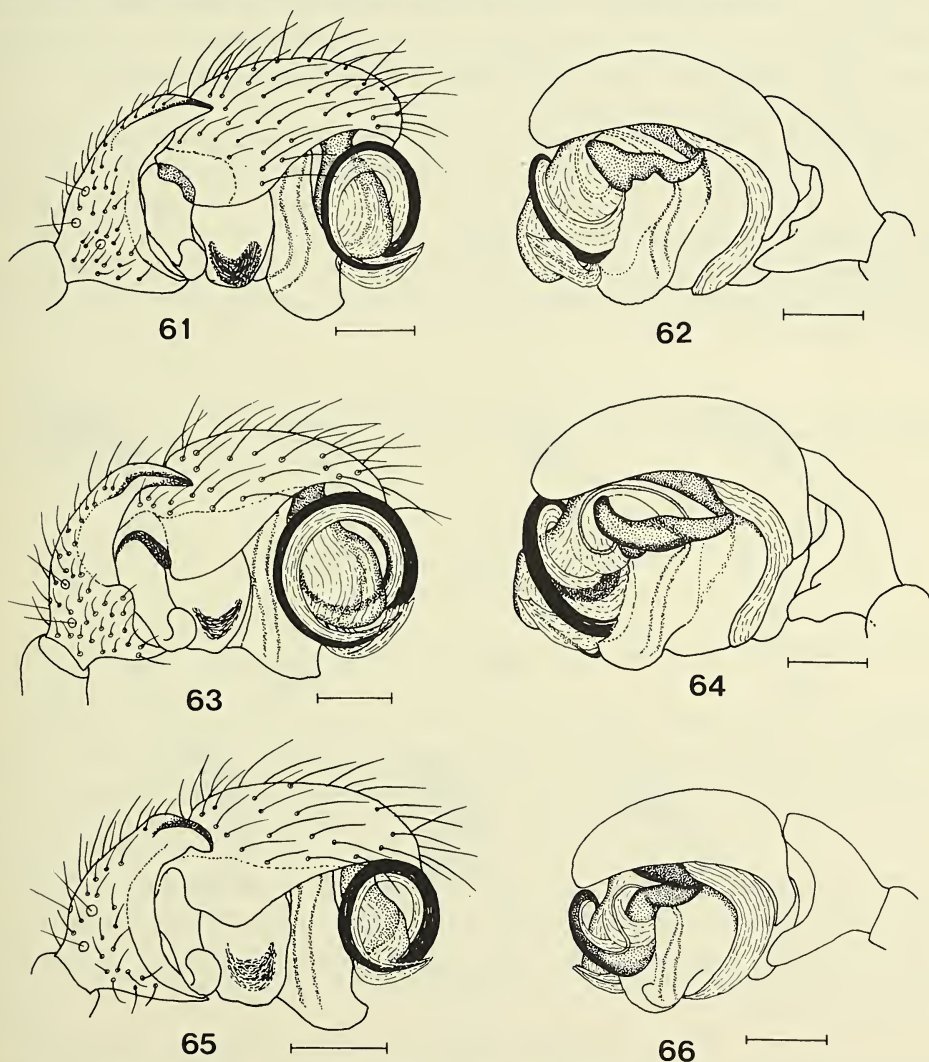
Walckenaeria capito: Simon 1884:823 (male, not female).

Wideria capito: Simon 1926:408, 411, 504; Roewer 1942:670; Locket and Millidge 1953:197; Bonnet 1959:4820; Wiehle 1960:134.

Walckenaeria (Walckenaeria) capito: Wunderlich 1972:375.

Prosopotheca incisa: Simon 1884:831 (male, not female) (misidentification).

Walckenaeria (Heteroprosopotheca) vidua Wunderlich 1972:377. NEW SYNONYM.



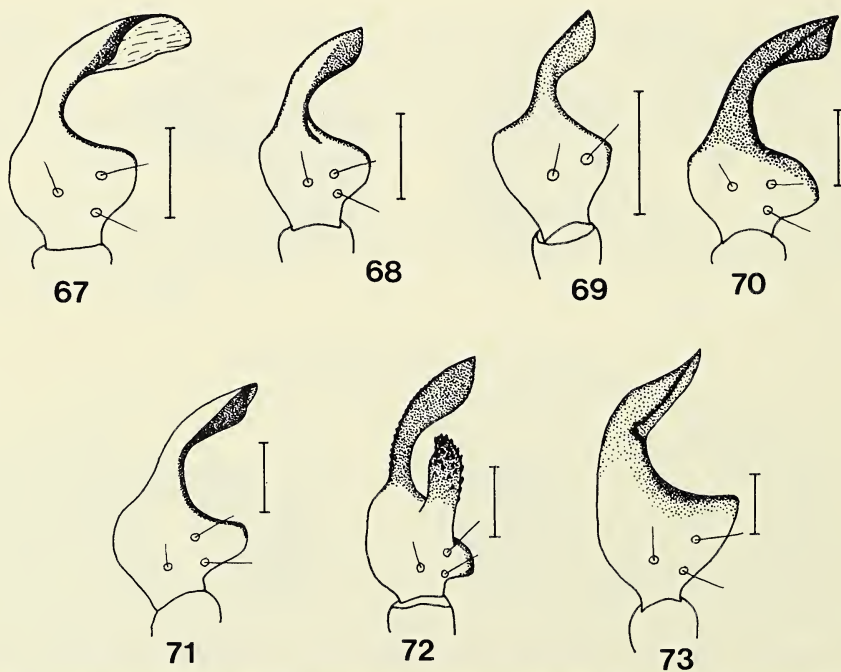
Figs. 61-66.—Male palps. 61, *W. iviei*, ectal; 62, *W. iviei*, mesal; 63, *W. rutilis*, ectal; 64, *W. rutilis*, mesal; 65, *W. rufula*, ectal; 66, *W. rufula*, mesal (Scale lines 0.1 mm).

Type.—Should be in Naturhistoriska Riksmuseet, Stockholm, but not located (T. Kronstedt, priv. comm.).

Description.—A single male only has been taken in N. America. In this specimen, and in Simon's male ("*Prosopotheca incisa*" male in MNHN, Paris), the large lobe which carries the posterior eyes has been broken off, possibly by the female during mating. The scar of this lobe in the Paris specimen was mistaken by Simon (1884:831) for the posterior median eyes, and was not commented upon by Wunderlich (1972: *W. vidua*). The N. American male is damaged (Figs. 99, 100) and the description given here is based on European specimens. Total length: female 3.0-3.5 mm, male 2.7-2.9 mm. Carapace: length: female 1.30-1.35 mm, male 1.45 mm. Brown to dark brown, with dusky markings and margins. The male carapace is raised anteriorly, and bears a large lobe which carries the posterior median eyes (Figs. 98, 100); the shape of the lobe shows some variation, the neck being sometimes quite narrow. The female carapace is also raised anteriorly (Fig. 101). Chelicerae: the lateral striae are moderately spaced in both sexes. Abdomen: grey to black. Sternum: light brown to orange-brown, suffused with black, particularly on margins. Legs: yellow to orange-brown. TmI: female 0.60-0.64, male 0.60-0.62. Male palp: Figs. 97, 99. Epigynum: Fig. 93.

Diagnosis.—The male of *W. capito* is diagnosed by the form of the carapace (Fig. 98), and by the form of the palpal tibia (Fig. 97). The female is diagnosed by the anterior elevation of the carapace (Fig. 101) coupled with the form of the epigynum (Fig. 93), which is distinct from that of any other species.

Distribution.—In Europe, this species has been recorded from most of the more northern and eastern countries. The only record from N. America is from Ontario (Map 7).



Figs. 67-73.—Male palpal tibiae, dorsal. 67, *W. spiralis*; 68, *W. arctica*; 69, *W. saniuana*; 70, *W. subvigilax*; 71, *W. fallax*; 72, *W. redneri*; 73, *W. castanea* (Scale lines 0.1 mm).

Natural History.—In Europe, adults of both sexes have been taken from May to October. The species has been recorded from mountains, up to ca. 1000 m, under stones, and at lower levels in herbage. The habitat of the Canadian specimen was not given.

Walckenaeria redneri, new species

Figs. 72, 94, 120; Map 1

This species is named in honor of J. H. Redner, who has captured several new species of *Walckenaeria*.

Type.—Male holotype from near Wasagaming, Riding Mountain National Park, Manitoba, 29 August 1979 (J. and M. Redner); deposited in CNC.

Description.—The two sexes were taken together. Total length: female 2.15 mm, male 2.0–2.1 mm. Carapace: length: female/male 1.0 mm. Pale brown to brown, suffused with black. Chelicerae: lateral striae moderately spaced in both sexes. Abdomen: grey to black. Sternum: brown, suffused with black, particularly on margins. Legs: pale brown to brown. TmI: female 0.55, male 0.50–0.60. Male palp: Figs. 72, 120; the embolic coil is large. Epigynum: Fig. 94; this is pale in color, and the spermathecae are widely separated. The rather pale colors of the specimens may indicate that they had only just attained maturity.

Diagnosis.—The male of *W. redneri* is diagnosed by the form of the palpal tibia (Fig. 72), which is unlike that of any other species, and confirmed by the form of the palp (Fig. 120). The female is diagnosed by the epigynum (Fig. 94), which is somewhat similar to that of *W. clavipalpe* (Fig. 95): these 2 species are readily distinguishable (see *W. clavipalpe* diagnosis).

Distribution.—Known only from Manitoba and Wisconsin (Map 1).

Natural History.—Adult males have been taken in August and October. The type was found in moss in a boggy area.

Walckenaeria clavipalpe, new species

Figs. 95, 117, 118; Map 1

Type.—Female holotype from Mt. Whiteface, New York, 13 September 1931 (C. R. Crosby); deposited in AMNH.

Description.—Only the female is known. Total length: female 3.0 mm. Carapace: length: female 1.30 mm. Orange-brown. Chelicerae: lateral striae very widely spaced (Fig. 117). Abdomen: grey-black. Sternum: orange-brown, with dusky markings and margins. Legs: yellow-brown. TmI: female 0.51. Female palp: tibia and tarsus swollen (Fig. 118). Epigynum: Fig. 95.

Diagnosis.—The female of *W. clavipalpe* is diagnosed by the epigynum (Fig. 95); this is fairly similar in appearance to that of *W. redneri* (Fig. 94), but *W. clavipalpe* is readily distinguished from this species by the much wider spacing of the cheliceral striae (Fig. 117) and by the swollen palpal segments (Fig. 118). *W. redneri* is also significantly smaller in size.

Distribution.—Known only from the type locality (Map 1).

Natural History.—The female was adult in September; nothing was recorded on habitat.

Walckenaeria castanea (Emerton), new combination

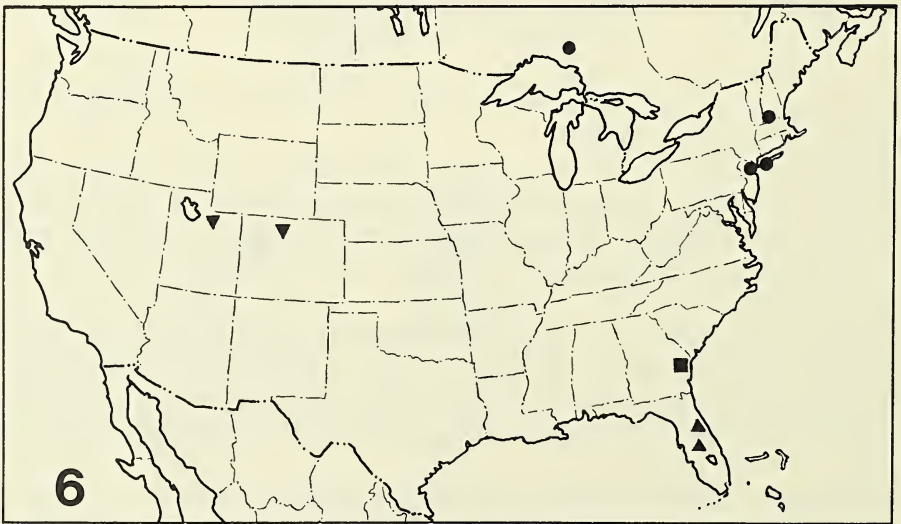
Figs. 73, 78, 79, 96, 105, 113, 114, 115; Map 8

Lophocarenum castaneum Emerton 1882:45.*Diplocephalus castaneus*: Crosby and Bishop 1928:1046.*Minyriolus castaneus*: Crosby and Bishop 1933:138; Roewer 1940:679; Kaston 1948:183; Bonnet 1957:2927.*Trachynella longidens* Holm 1960:124 (type female, MCZ, examined). NEW SYNONYM.*Trachynella nudipalpis*: Hackman 1954:67 (probably) (misidentification) (not *Erigone nudipalpis* Westring): I have not seen the specimen.

Type.—Male holotype from Beverly, Essex Co., Massachusetts, 9 November 1879; in MCZ, examined.

Description.—Total length: female 2.6-3.9 mm, male 2.45-3.0 mm. Carapace: length: female 1.10-1.45 mm, male 1.15-1.35 mm. Pale brown to chestnut brown, sometimes rather darker anteriorly. The male has anteriorly a small lobe with large holes and sulci on its sides (Figs. 113, 114); the lobe carries the posterior median eyes. The males from the far northwest (*T. longidens*) have the lobe slightly broader and the posterior median eyes marginally smaller (Fig. 115). Chelicerae: the lateral striae are moderately spaced. Abdomen: grey to black. Sternum: orange or orange-brown, with blackish margins. Legs: orange-brown to chestnut brown. TmI: female 0.43-0.45, male 0.42-0.47. Male palp: Figs. 73, 78, 79. The embolic coil is large; in the northwestern males (*longidens*) the coil tends to be slightly larger in diameter than shown in Fig. 73, but there is some variation in the diameter even amongst the eastern males. Female palp: tibia sometimes swollen distally, but less so than in *W. clavipalpe*. Epigynum: Figs. 96, 105; this bears a close resemblance to that of the European species *Walckenaeria nudipalpis* Westr.

The populations from the far northwest show minor differences from those of the centre and east, but these differences do not appear large enough or consistent enough to justify the retention of *W. longidens* as a separate species; there is no detectable difference between the internal genitalia of females from difference areas, nor can any stable differences be recognized in the male palps.

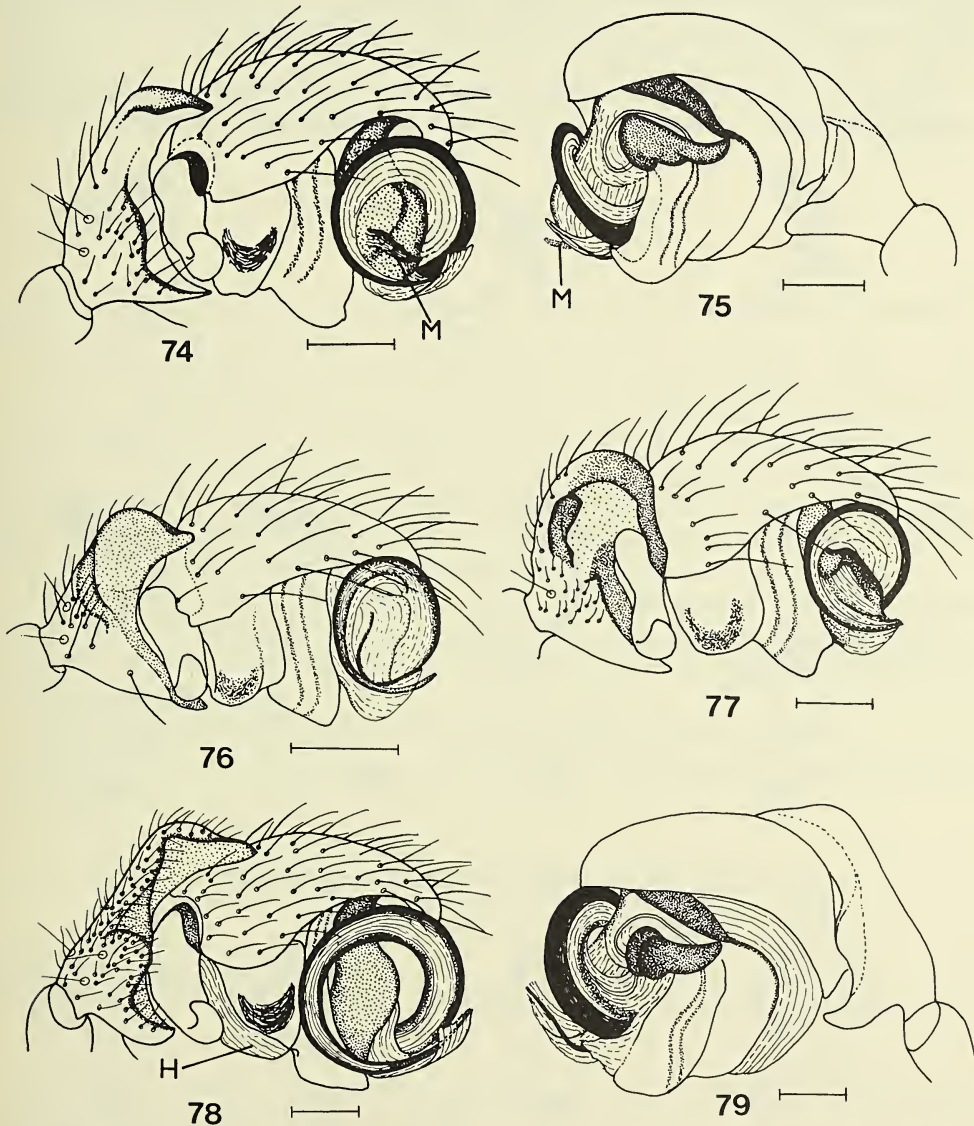


Map 6.—North America. Distribution of *W. digitata* (circles), *W. floridiana* (triangles), *W. maesta* (inverted triangles) and *W. dixiana* (square).

Diagnosis.—The male of *W. castanea* is diagnosed by the lobe on the carapace (Fig. 113), and confirmed by the form of the palpal tibia (Fig. 73) and the palpal organs (Fig. 78). The female is diagnosed by the epigynum (Fig. 96); the divergent, feather-like form of the anterior ducts seen through the integument is distinctive.

Distribution.—This species is widely distributed throughout N. America, apart from southern areas (Map 8).

Natural History.—Both sexes have been taken in practically every month of the year. Habitats recorded are a sphagnum bog, a pine swamp, moss in a boggy area, woods, tall grass, a soil sample, and under snow in February.



Figs. 74-79.—Male palps. 74, *W. crocea*, ectal; 75, *W. crocea*, mesal; 76, *W. gertschi*, ectal; 77, *W. aenea*, ectal; 78, *W. castanea*, ectal; 79, *W. castanea*, mesal; Abbreviations: H, haematodocha; M, membrane (Scale lines 0.1 mm).

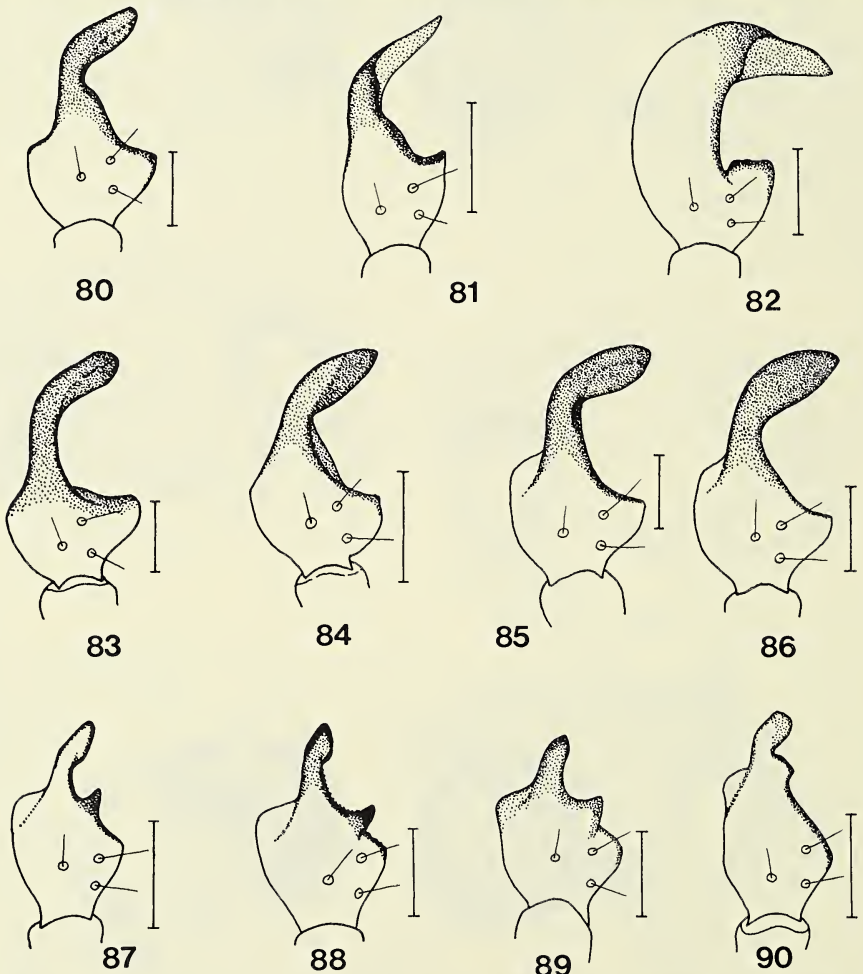
Walckenaeria dixiana (Chamberlin and Ivie), new combination
Figs. 87, 119, 122, 127; Map 6

Cornicularia dixiana Chamberlin and Ivie 1944:68.

Type.—Male holotype from 3 miles southeast of Savannah, Chatham Co., Georgia, 8 April 1943 (W. Ivie); in AMNH, examined.

Description.—Total length: female 1.9-1.95 mm, male 1.5-1.65 mm. Carapace: length: female 0.70-0.78 mm, male 0.70 mm. Brown, with dusky markings and margins. Chelicerae: lateral striae fairly widely separated in both sexes. Abdomen: whitish grey, suffused with black posteriorly around the spinners. Sternum: yellow, suffused with black. Legs: yellow-brown to orange. TmI: female 0.50, male 0.46. Male palp: Figs. 87, 119, 122; the embolic coil is rather small. Epigynum: Fig. 127.

Diagnosis.—The male of *W. dixiana* is diagnosed by the form of the palpal tibia (Fig. 87) and of the palp, which has the embolic coil relatively small in diameter (Fig. 119).



Figs. 80-90.—Palpal tibiae, dorsal. 80, *W. iviei*; 81, *W. gertschi*; 82, *W. aenea*; 83, *W. rutilis*; 84, *W. rufula*; 85, *W. crocea*; 86, *W. crocea*, another specimen; 87, *W. dixiana*; 88, *W. digitata*; 89, *W. maesta*; 90, *W. mexicana* (Scale lines 0.1 mm).

The abdominal coloration (pale grey-white, suffused with black around the spinners) offers confirmation of the identity. The male of *W. floridiana* does not seem to be distinguishable from that of *W. dixiana*. The males of *W. digitata* and *W. maesta* are also very similar to *W. dixiana*, but in both of these species the palps are significantly larger in size, there are small differences in the form of the palpal tibia (Figs. 88, 89 cf Fig. 87), and the tailpiece is longer (Fig. 124 cf. Fig. 122); the geographical distributions are also different from that of *W. dixiana*. The female of *W. dixiana* is diagnosed by the epigynum, which is pale in color and simple in form (Fig. 127); only *W. digitata* has a somewhat similar epigynum (Fig. 129), but this species is larger in size, the proportions of the legs are different (e.g. tibia I 1/d in *W. dixiana* is 5.5-6, in *W. digitata* is 7-7.5), and the geographical range appears to be different. The epigyna of *W. floridiana* (Fig. 128), *W. maesta* (Fig. 130) and *W. aurata* (Fig. 131) are sufficiently unlike *W. dixiana* to make confusion unlikely.

Distribution.—Known only from the type locality (Map 6).

Natural History.—Both sexes were taken in April; nothing was recorded on habitat.

Walckenaeria floridiana, new species

Fig. 128; Map 6

Type.—Female holotype from 2 miles south of Orange City, Volusia Co., Florida, 9 December 1962 (W. Ivie); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 1.90 mm, male 1.70 mm. Carapace: length: female 0.76 mm, 0.67 mm. Pale orange in female, brown to orange-brown with dusky markings and margins in male. Chelicerae: the lateral striae are moderately spaced in female, more widely spaced in male. Abdomen: practically white in female, grey in male, in both sexes suffused with black around the spinners. Sternum: pale yellow, with dusky margins. Legs: pale orange. TmI: female 0.50, male 0.50-0.56. Male palp: not distinguishable from that of *W. dixiana*. Epigynum: Fig. 128.

Diagnosis.—The male of *W. floridiana* appears to be indistinguishable from *W. dixiana* (see *W. dixiana* diagnosis). The female is diagnosed by the epigynum (Fig. 128), which is sufficiently distinct from that of *W. dixiana* (Fig. 127) and the other related species to make confusion unlikely.

Distribution.—Known only from two localities in Florida (Map 6).

Natural History.—Both sexes were taken in March and December; nothing was recorded on habitat.

Walckenaeria digitata (Emerton), new combination

Figs. 88, 107, 129; Map 6

Tmeticus digitatus Emerton 1913:256.

Prosopotheca digitata: Crosby and Bishop 1928:1051; Roewer 1942:665; Kaston 1948:169; Bonnet 1958:3782.

Type.—Male holotype from Cold Spring Harbor, Long Island, New York, 22 June 1903 (J. H. Emerton); in AMNH, examined.

Description.—The female, described here for the first time, was taken in the same general area as the male, but not with a male; hence its identity cannot be regarded as completely certain. Total length: female 2.40-2.80 mm, male 1.80 mm. Carapace: brown,

with dusky markings and margins. Chelicerae: lateral striae widely separated in both sexes. Abdomen: uniformly black in the male, grey suffused with black posteriorly around the spinners in the female. Sternum: brown, suffused with black. Legs: orange-brown. TmI: female 0.50-0.53, male 0.53. Male palp: Fig. 88; apart from their larger size, the palpal organs are practically identical with those of *W. dixiana*. Epigynum: Figs. 107, 129.

Diagnosis.—The male of *W. digitata* is very similar to those of *W. dixiana* and *W. floridiana* (see *W. dixiana* diagnosis), and to that of *W. maesta*; from the latter species, *W. digitata* male can be distinguished by a small difference in the palpal tibiae (Fig. 88 cf. Fig. 89) and probably by the geographical distribution. The epigyna of *W. digitata* and *W. dixiana* are very similar (Fig. 129 cf. Fig. 127), but appear to be distinguishable by the rather wider posterior "plate" in *W. digitata*, and the species can also be separated by a larger size of *W. digitata*. The epigyna of the related species *W. maesta* (Fig. 130), *W. floridiana* (Fig. 128) and *W. aurata* (Fig. 131) are not likely to be confused with that of *W. digitata*.

Distribution.—*W. digitata* is known only from four localities in a limited area of the northeast of N. America (Map 6).

Natural History.—Males have been taken in June, females in July. Nothing was recorded on habitat.

Walckenaeria maesta, new species

Figs. 89, 121, 124, 130; Map 6

Type.—Female holotype from west of Fort Collins, Lorimer Co., Colorado, 7,300 ft., 28 July 1946 (C. C. Hoff); deposited in AMNH.

Description.—The male described here was taken in Utah, some 5° west of the type locality; until the two sexes are taken together, the identity of the male cannot be regarded as completely certain. Total length: female 2.55 mm, male 1.90 mm. Carapace: length: female 1.0 mm, male 0.90 mm. Brown, heavily suffused with black anteriorly and on margins. Chelicerae: lateral striae moderately widely separated in both sexes. Abdomen: grey-black to black. Sternum: brown, suffused with black. Legs: yellow to orange-brown. TmI: female 0.50, male 0.48. Male palp: Figs. 89, 121, 124; the palpal organs are closely similar to those of *W. dixiana*. Epigynum: Fig. 130.

Diagnosis.—The palp of *W. maesta* (Fig. 121) is very similar to that of *W. dixiana* (Fig. 119) and *W. floridiana*, but is larger in size; the tegular duct on the ectal side is relatively narrower, and the tailpiece is longer (Fig. 124 cf. Fig. 122). The abdomen of *W. maesta* is darker in color than in *W. dixiana* or *W. floridiana*. *W. maesta* male is separable from *W. digitata* only by the relatively narrower tegular duct on the ectal side. The female of *W. maesta* is diagnosed by the epigynum (Fig. 130), which should be distinguishable from those of the related species (Figs. 127, 128, 129, 131); the geographical distribution should be also be taken into account.

Distribution.—Known only from Colorado and Utah (Map 6).

Natural History.—The female was taken in July, the male in June. The type habitat was at ca. 2200 m, but no further details were given.

Walckenaeria aurata, new species

Fig. 131; Map 5

Type.—Female holotype from Tepoztlan, Morelos, Mexico, 5 May 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Only the female is known. Total length: female 2.05 mm. Carapace: length: female 0.75-0.80 mm. Orange. Chelicerae: lateral striae moderately spaced. Abdomen: almost white, faintly blackened around spinners. Sternum: yellow-orange. Legs: orange-brown. TmI: female 0.45-0.47. Epigynum: Fig. 131.

Diagnosis.—*W. aurata* female is diagnosed by the epigynum (Fig. 131); *W. maesta* has the epigynum (Fig. 130) somewhat similar in shape, but this species is darker in color and has a different geographical distribution.

Distribution.—Known only from the type locality in Mexico (Map 5).

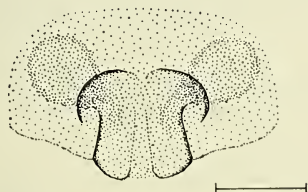
Natural History.—The females were taken adult in May; nothing was recorded on habitat.

Walckenaeria mexicana, new species

Figs. 90, 123; Map 5

Type.—Male holotype from 6 miles north east of El Salto, Durango, Mexico, 11 August 1947 (W. J. Gertsch); deposited in AMNH.

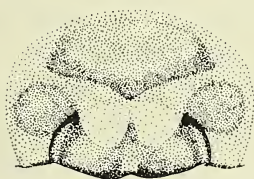
Description.—There is only the type specimen, which has the abdomen missing. Carapace: length: male 0.80 mm. Orange, slightly darkened anteriorly. Chelicerae: lateral striae fairly well spaced. Sternum: orange-yellow. Legs: orange-brown. TmI: male 0.40.



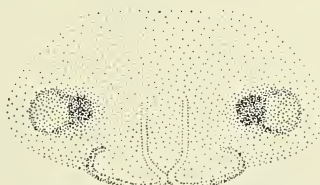
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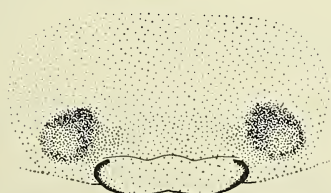
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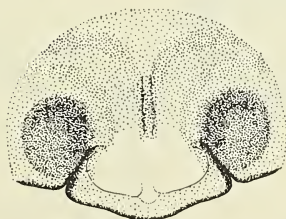
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94



95



96

Figs. 91-96.—Epigyna. 91, *W. gertschi*; 92, *W. aenea*; 93, *W. capito*; 94, *W. redneri*; 95, *W. claviger*; 96, *W. castanea* (Scale lines 0.1 mm).

Male palp: Figs. 90, 123; the embolic coil is small. There is a possibility that this is the male of *W. aurata*; it is considered unlikely that it is the male of *W. discolor*, which was taken in the same locality (but at a different time), because of the wide discrepancy in the values of TmI.

Diagnosis.—This species is diagnosed by the form of the palpal tibia (Fig. 90), which differs from those of the other species of the *dixiana* type; confirmation is given by the palp (Fig. 123), in which the embolic coil is smaller in diameter than in the other species.

Distribution.—Known only from the type locality in Mexico (Map 5).

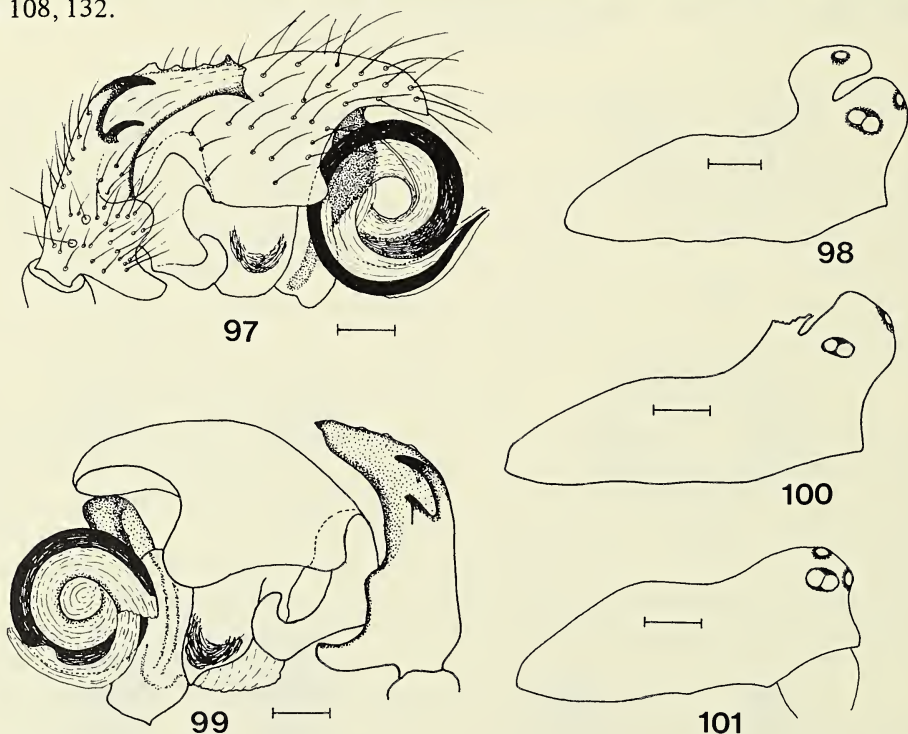
Natural History.—The male was adult in August; nothing was recorded on habitat.

Walckenaeria puella, new species

Figs. 108, 132; Map 5

Type.—Female holotype from Alice, Jim Wells Co., Texas, 15-30 May 1961 (R. O. Albert); deposited in MCZ.

Description.—Only the female is known. Total length: female 2.0 mm. Carapace: length: female 0.75 mm. Pale yellow, shading to pale orange anteriorly. Chelicerae: lateral striae moderately spaced. Abdomen: practically white, suffused with grey around the spinners. Sternum: pale yellow. Legs: pale yellow-brown. TmI: female 0.51. Epigynum: Figs. 108, 132.



Figs. 97-101.—*W. capito*. 97, male palp, ectal, European specimen; 98, male carapace, lateral, European specimen; 99, male palp, left, damaged, Canadian specimen; 100, male carapace, Canadian specimen; 101, female carapace, lateral, European specimen (Scale lines, 97, 99, 0.1 mm; 98, 100, 101, 0.2 mm).

Diagnosis.—*W. puella* is diagnosed by its pale color and by the epigynum (Fig. 132), which is sufficiently different from those of all other species to make confusion unlikely.

Distribution.—Known only from the type locality (Map 5).

Natural History.—The female was adult in May; nothing was recorded on habitat.

Walckenaeria blanda, new species
Figs. 35, 45, 52; Map 2

Type.—Female holotype from Rustler Park, Chiricahua Mts., Cochise Co., Arizona, 23 May 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Only the female is known. Total length: female 2.35-2.45 mm. Carapace: length: female 0.90-0.95 mm. Orange to orange-brown, with dusky markings and ocular area suffused with black. Abdomen: grey-black. Sternum: orange, with dusky markings and margins. Legs: orange to orange brown. TmI: female 0.50. Epigynum: Figs. 35, 45, 52. In the absence of the male, it is uncertain whether *W. blanda* is correctly placed in the *acuminata* species group; the internal genitalia of the female show some similarities to those of *W. directa* (Fig. 178).

Diagnosis.—*W. blanda* can be diagnosed by the epigynum (Fig. 35), which differs sufficiently from those of other species to make confusion unlikely. The diagnosis can be confirmed by the form of the internal genitalia (Figs. 45, 52).

Distribution.—The species is known from mountainous areas in Arizona and New Mexico.

Natural History.—Adult females have been taken in May, August and September; nothing was recorded on habitat.

directa Group

The males of this group have closely similar palpal tibiae and palpal organs, but diagnosis is fairly easy on the basis of the form of the carapace horn or lobe. Most of the females have virtually identical epigyna; the distinct differences depicted in the figures given by Crosby and Bishop (1931) appear to be exaggerated, and with the museum material which I have examined the epigyna of most species show no real or constant differences. The females of most species can be diagnosed satisfactorily on the basis of other characters, but there are occasions when the diagnosis is uncertain unless the female is taken with the male.

Partial keys to the species

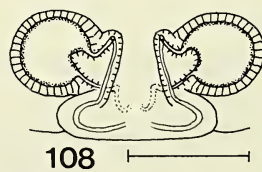
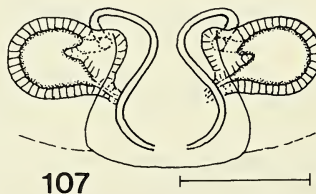
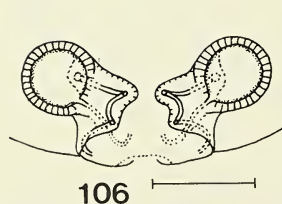
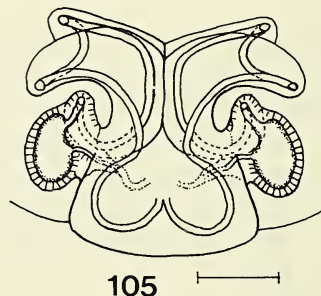
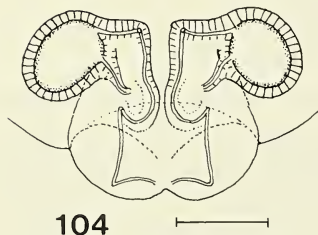
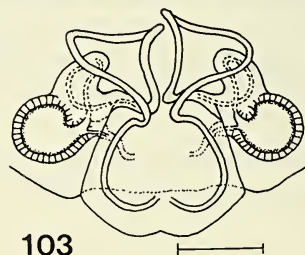
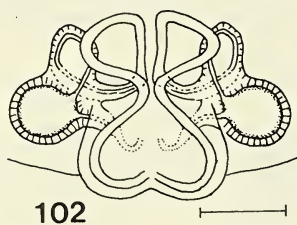
Males

- 1. Carapace with horn projecting forwards from the ocular area (e.g. Figs. 142, 145, 152) 2
 - Carapace without a forward-projecting horn 3
- 2. Horn relatively long (Figs. 142, 143, 144)
 - *directa*, *subdirecta*, *communis*, *indirecta* (see species descriptions)
 - Horn shorter (Figs. 145, 152) *brevicornis*, *breviaria* (see species descriptions)

3. Carapace more or less smoothly raised anteriorly (Figs. 147, 149, 150, 153)
 *pallida*, *subpallida*, *prominens*, *carolina* (see species descriptions)
 Carapace with small knob-like lobe in ocular area (Figs. 151, 154) 4
4. Lobe distinctly forked in anterior view (Fig. 162) *dondalei*
 Lobe not forked (Fig. 163) *oregona*

Females

1. Pedicel relatively long and exposed (Fig. 167) 2
 Pedicel short and less conspicuous 3
2. Abdomen grey to black; tibia I 1/d 5.5-6 *indirecta*
 Abdomen whitish, darkened around spinners; tibia I 1/d 7.5-9
 *pallida*, *subpallida* (see species descriptions)
3. Carapace darkened in cephalic area
 *communis*, *brevicornis*, *dondalei* (see species descriptions)
 Carapace not darkened in cephalic area 4
4. Epigynum Fig. 177; carapace raised anteriorly (Fig. 166) *carolina*
 Epigynum Fig. 175; carapace less sharply raised
 *directa*, *subdirecta*, *oregona* (see species descriptions)



Figs. 102-108.—Female genitalia, cleared, dorsal. 102, *W. iviei*; 103, *W. rutilis*; 104, *W. aenea*; 105, *W. castanea*; 106, *W. gertschi*; 107, *W. digitata*; 108, *W. puella* (Scale lines 0.1 mm).

Walckenaeria directa (O.P.-Cambridge)

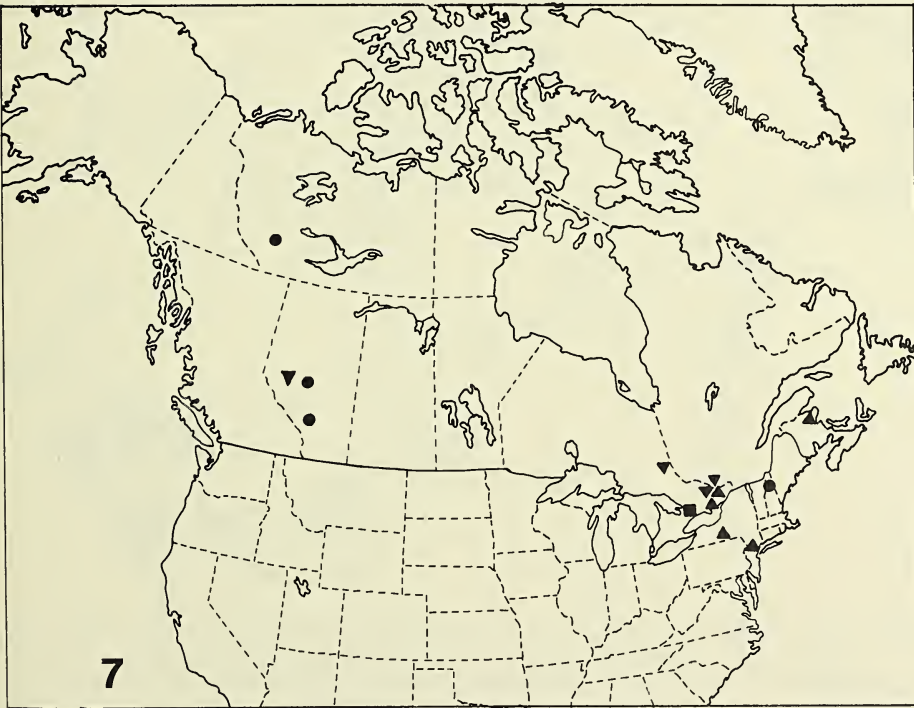
Figs. 133, 137, 138, 139, 142, 168, 175, 178, 303, 305, 308, 310; Map 9

Erigone directa O.P.-Cambridge 1874:439.*Cornicularia directa*: Emerton 1882:40 (in part); Crosby and Bishop 1931:367 (in part); Roewer 1942:663 (in part); Kaston 1948:166 (in part); Bonnet 1956:1223 (in part).*Walckenaeria (Pseudoprosopotheca) directa*: Wunderlich 1972:383 (in part).

In the past, *W. directa* has not been differentiated from its sibling species *W. sub-directa*.

Type.—Male and female syntypes in the Hope Entomological Collections, Oxford; examined. The type locality is not given.

Description.—Total length: female 2.1-2.9 mm, male 2.0-2.7 mm. The largest specimens have been those taken in Alaska. Carapace: length: female 0.95-1.15 mm, male 0.90-1.15 mm (excluding horn). Deep chestnut brown, with dusky margins and markings. The male bears anteriorly a horn (Figs. 139, 142, 303) which comprises a large upper section and a small lower section separated by a cleft. The anterior hairs on the horn appear under the binocular microscope to be "spatulate", but are actually trifurcate, arising from deep pits (Figs. 303, 305); the simple hairs on the posterior part of the horn are all reflexed (Fig. 142). Chelicerae: the lateral striae are moderately widely spaced in the female (Fig. 308), but more closely spaced in the male (Fig. 310). Abdomen: grey to black. Sternum: orange to chestnut brown, with blackish margins; the surface is smooth and shiny but marked to a variable degree with minute pits. Legs: orange to brown. TmI: female 0.45-0.55, male 0.48-0.56. Female palp: tibia and tarsus usually darker in color

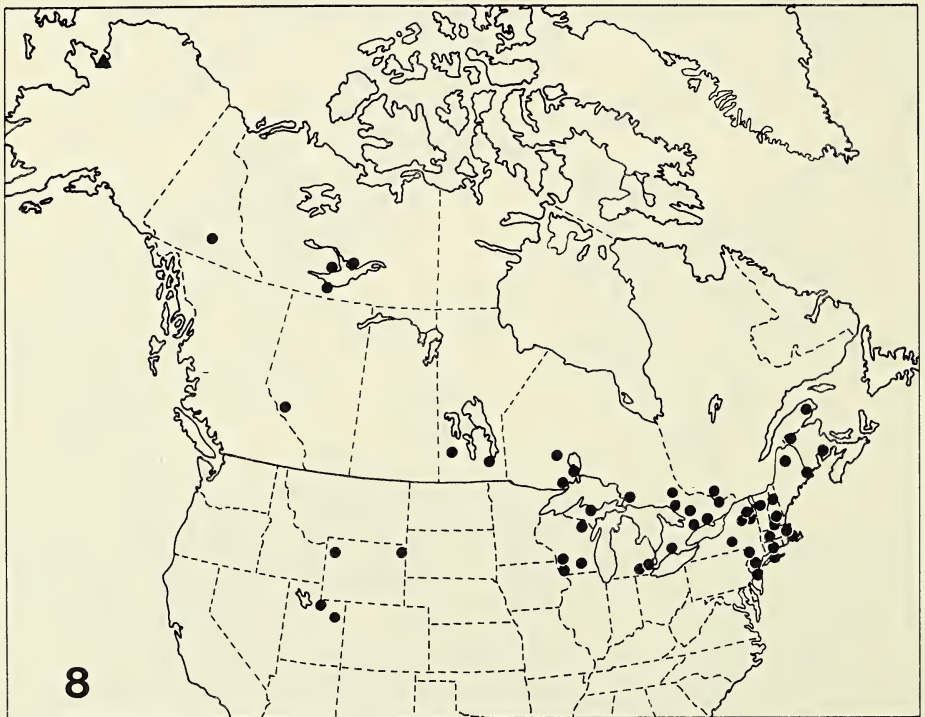


Map 7.—North America. Distribution of *W. arctica* (circles), *W. microspiralis* (triangles), *W. fallax* (inverted triangles) and *W. capito* (square).

than the legs. Male palp: Figs. 133, 137, 138, 168; anteriorly the ED has a blunt point, often colorless and transparent, as in *W. pallida* (Fig. 134). Epigynum: Figs. 175, 178.

Diagnosis.—The male of *W. directa* is diagnosed by the carapace horn. The horns (which show small intraspecific variations in shape and length) are generally similar in *W. directa*, *W. subdirecta*, *W. communis* and *W. indirecta*: the distinguishing characters are as follows. In *W. directa* (Figs. 139, 142) and *W. subdirecta* the dorsal hairs extend posteriad almost to the posterior median eyes, all the hairs being reflexed. In *W. communis* (Figs. 140, 143) the hairs extend scarcely to the base of the horn, and posteriorly the hairs incline forwards; the carapace is usually more orange in *W. communis* than in *W. directa*. In *W. indirecta* (Figs. 141, 144) the horn is rather shorter, the spatulate hairs extend posteriad along the whole length of the horn, and the posterior row of eyes is strongly procurved; this species also has a relatively long sclerotized pedicel, more or less as in *W. pallida* (Fig. 167). *W. directa* and *W. subdirecta* males are separated by the cheliceral file, the striae being very closely spaced in *W. subdirecta* (Fig. 311) and significantly more widely spaced in *W. directa* (Fig. 310); the differences are clearly visible in the optical microscope. The female of *W. directa* is grouped with *W. subdirecta* and *W. oregona* in the key. The separation of these three species is not possible by the epigyna, but is based on the spacing of the cheliceral file. The striae are closely spaced in *W. subdirecta* (Fig. 309) and more widely spaced in *W. directa* (Fig. 308); in *W. oregona* the spacing is significantly wider again than in *W. directa*, and with experience, with authentic specimens for comparison, the separation of these two species is not difficult. The distribution of *W. oregona* (west coast only) should also be borne in mind for diagnosis.

Distribution.—Widely distributed throughout N. America apart from the extreme south (Map 9). *W. directa* appears to be sympatric with *W. subdirecta* in several localities.



Map 8.—North America. Distributions of *W. castanea* (circles) and *W. fraudatrix* (triangle).

Natural History.—Adults of both sexes have been taken in all months except January. The only habitats recorded are in grass, in leaf litter, in hardwood litter, amongst shrubs (pitfall), and it has been observed ballooning in October.

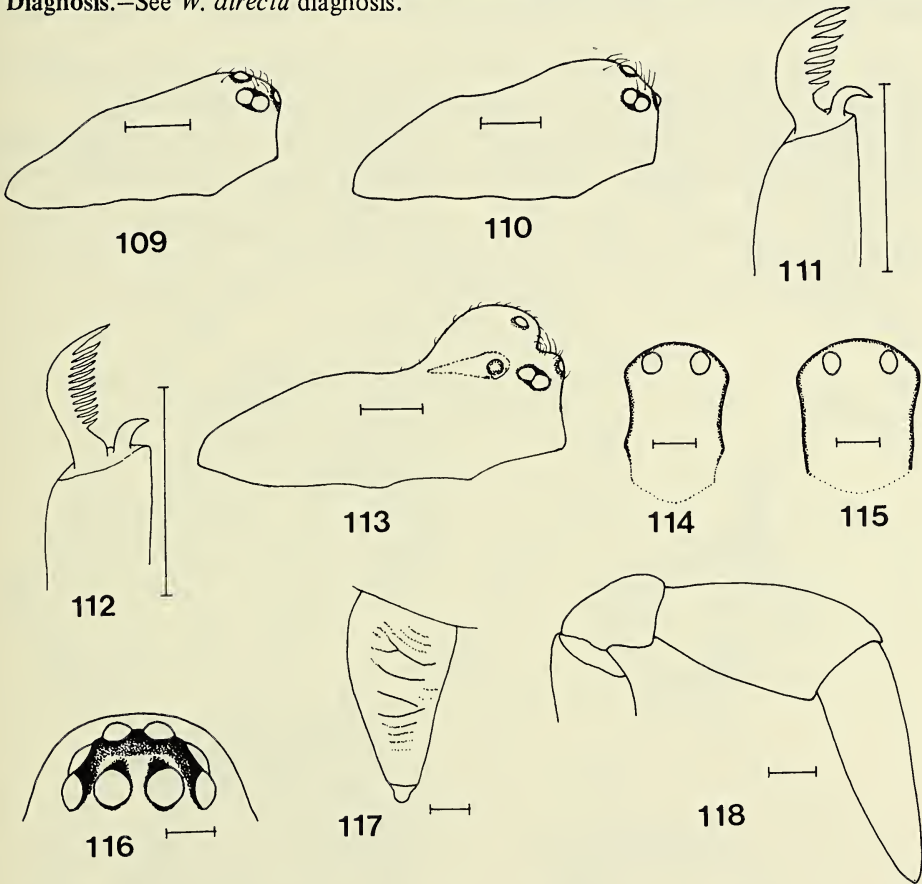
Walckenaeria subdirecta, new species

Figs. 304, 309, 311; Map 10

Type.—Male holotype from east of Jamison (Horseshoe Bend, Neshaminy Creek), Pennsylvania, 28 September 1953 (W. Ivie); deposited in AMNH.

Description.—In size, color and genitalia this species is not distinguishable from *W. directa*. Carapace: Fig. 304; the horn is probably not distinguishable from that of *W. directa*. Chelicerae: the lateral striae are close together in the female (Fig. 309), very close together in the male (Fig. 311). Legs: TmI: female 0.50-0.58, male 0.51-0.60.

Diagnosis.—See *W. directa* diagnosis.



Figs. 109-118.—109, *W. spiralis*, male carapace, lateral; 110, *W. microspiralis*, male carapace, lateral; 111, *W. communis*, female, tarsal claw, leg I; 112, *W. spiralis*, female, tarsal claw, leg I; 113, *W. castanea*, male carapace, lateral; 114, *W. castanea*, male carapace lobe, dorsal; 115, *W. castanea*, male carapace lobe, dorsal, Alberta specimen; 116, *W. gertschi*, female eyes, dorsal; 117, *W. clavipalpe*, female, left chelicera; 118, *W. clavipalpe*, female palp (Scale lines 0.1 mm, except 109, 110, 113, 0.2 mm).

Distribution.—Fairly widely distributed throughout N. America (Map 10), though noticeably less so (on current knowledge) than *W. directa* (Map 9). The species appears to be sympatric with *W. directa* in several localities.

Natural History.—Adult females have been taken from March to December, males in January and from March to October. Habitats recorded are in grass and meadows, in woods, in bog, on dunes amongst pines, in leaf litter, under stones and on low vegetation (sweeping).

Walckenaeria communis (Emerton)
Figs. 111, 140, 143, 164, 306; Map 11

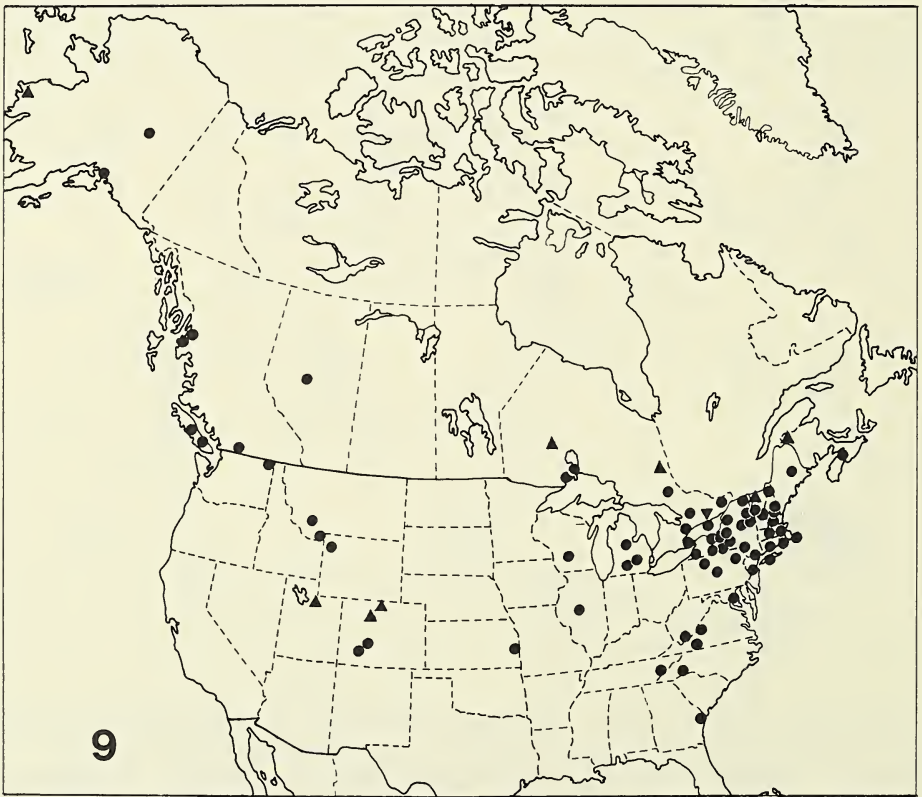
Cornicularia communis Emerton 1882:41; Crosby and Bishop 1931:366; Roewer 1942:663; Kaston 1948:165; Bonnet 1956:1221.

Walckenaeria (Pseudoprosopotheca) communis: Wunderlich 1972:383.

Cornicularia varipes Banks 1900:479; female type from NMNH examined. NEW SYNONYM.

Type.—Male and female syntypes from Clarendon Hills, Hyde Park, Suffolk Co., Massachusetts, 4 March 1878; in Emerton Collection, MCZ, examined.

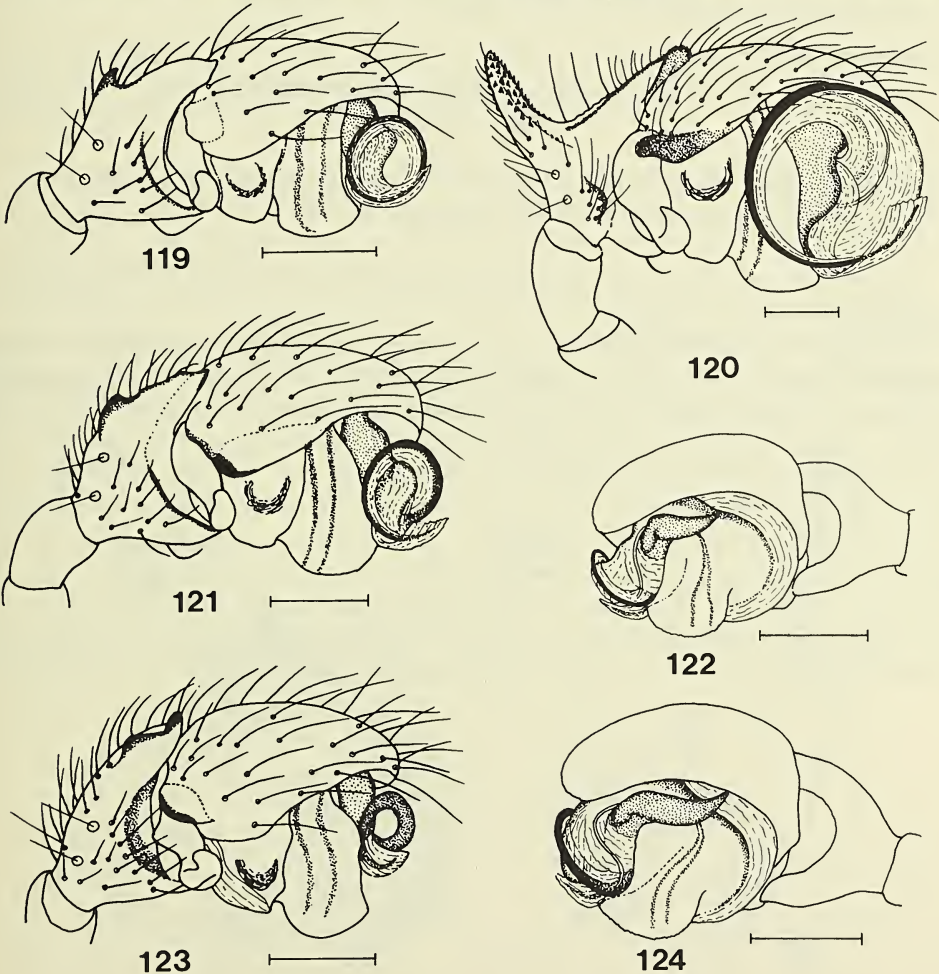
Description.—Total length: female 2.5-3.2 mm, male 2.45-3.1 mm. Carapace: length: female 0.95-1.2 mm, male 1.2-1.3 mm (excluding horn). Orange to deep reddish orange in



Map 9.—North America. Distributions of *W. directa* (circles), *W. cuspidata brevicula* (triangles) and *W. dondalei* (inverted triangle).

female, darkened anteriorly, often to almost black. The male carapace is similarly colored, but the anterior darkening is much less pronounced or even absent. Recently molted specimens are paler in color, but the female carapace seems always to be darkened anteriorly. The posterior hairs on the male horn (Figs. 140, 143) are short and directed forwards. Chelicerae: the lateral striae in the female are somewhat less widely spaced than in *W. directa*, but further apart than in *W. subdirecta*; in the male, the striae are very closely spaced, even more so than in *W. subdirecta*. There is little variation in the spacing of the striae throughout the whole range of the species. Abdomen: grey to black. Sternum: pale brown to orange, with dusky margins; the surface is smooth and shiny with no pits. Legs: yellow-brown to orange, with the three distal segments darkened to a variable degree in the female. TmI: female/male 0.50-0.62. Female palp: tibia and tarsus usually darkened. Male palp: indistinguishable from that of *W. directa*. Epigynum: indistinguishable from that of *W. directa*.

Diagnosis.—The male of *W. communis* is diagnosed by the carapace horn: see *W. directa* diagnosis. The female of *W. communis* is associated with *W. brevicornis* and *W.*



Figs. 119-124.—Male palps. 119, *W. dixiana*, ectal; 120, *W. redneri*, ectal; 121, *W. maesta*, ectal; 122, *W. dixiana*, mesal; 123, *W. mexicana*, ectal; 124, *W. maesta*, mesal (Scale lines 0.1 mm).

dondalei in the key. The epigynum of *W. communis* is indistinguishable from that of *W. dondalei*, but is distinguishable from that of *W. brevicornis* in specimens of the latter where the dark markings enclosing the posterior area extend forwards as converging lines as shown in Fig. 176. Not all females of *W. brevicornis* have this distinctive form of the epigynum, which in any case is liable to fade in preserved specimens, and hence the separation of *W. communis* from *W. brevicornis* by the epigynum is not always possible. In *W. communis* female there is usually some darkening of the distal segments of the legs, which is absent in *W. brevicornis* and *W. dondalei*, and the carapace of *W. communis* is slightly more raised behind the eyes (Fig. 164) than in these two species (Fig. 165); *W. communis* also tends to be larger in size. All these differences are small, and the separation of the females of these three species is not reliable in some instances.

Distribution.—*W. communis* is widely distributed throughout N. America, except for the more southerly parts (Map 11).

Natural History.—Adults of both sexes have been taken in all months except January. The only habitats recorded are a lake shore, wet grass, and moss in fir woods; it has also been recovered from a frog's stomach in Alaska.

Walckenaeria breviaria (Crosby and Bishop)

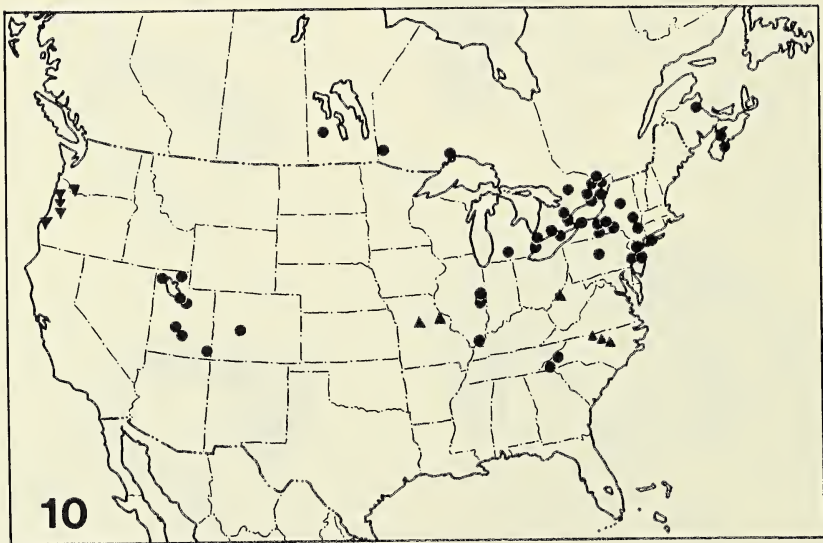
Fig. 145; Map 12

Cornicularia breviaria Crosby and Bishop 1931:362; Roewer 1942:662; Bonnet 1956:1221.

Walckenaeria (Pseudoprosopotheca) breviaria: Wunderlich 1972:283.

Type.—Male holotype from Interlaken, Seneca Co., New York, 26 November 1915 (Bishop); in AMNH, examined.

Description.—Only the male is known. Total length: male 2.1 mm. Carapace: length: male 1.0 mm. Chestnut brown, with dusky markings. The horn (Fig. 145) resembles a shortened version of that of *W. directa*. Chelicerae: the lateral striae are fairly closely



Map 10.—North America. Distributions of *W. subdirecta* (circles), *W. carolina* (triangles) and *W. oregona* (inverted triangles).

spaced. Abdomen: black, with faint paler chevrons posteriorly. Sternum: orange, with blackish margins; a few tiny pits are present. Legs: orange-yellow. TmI: male 0.50. Male palp: identical with that of *W. directa*. It must be questionable whether *W. breviarua* is a good species; it is possible that the male is only an abnormal specimen of *W. directa* or *W. subdirecta*.

Diagnosis.—*W. breviarua* male is diagnosed by the form of the carapace horn (Fig. 145), which is rather similar to that of *W. brevicornis* (Fig. 152). These two species can be separated by the palps, which in *W. breviarua* are as in *W. directa* (tibia Fig. 168, membraneous part of SA Fig. 133; cf. Figs. 169, 135 for *W. brevicornis*); an additional difference is that the carapace of *W. brevicornis* is somewhat darkened anteriorly.

Distribution.—Known only from the type locality (Map 12).

Natural History.—The male was adult in November; nothing was recorded on habitat.

Walckenaeria pallida (Emerton)

Figs. 134, 147, 148, 155, 166, 307; Map 13

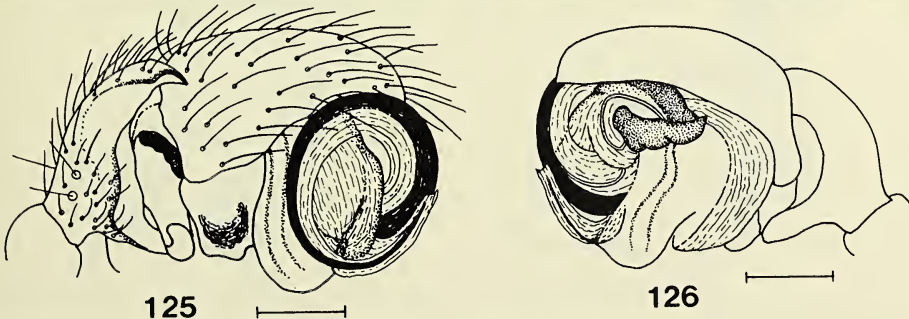
Cornicularia pallida Emerton 1882:42; Crosby and Bishop 1931:372 (in part); Roewer 1942:663; (in part); Kaston 1948:167 (in part); Bonnet 1956:1225 (in part).

Walckenaeria (Pseudoprosopotheca) pallida: Wunderlich 1972:383.

In the past, *W. pallida* has not been differentiated from *W. subpallida*, and hence the records given in some of the above papers may not be correct.

Type.—Male and female syntypes from New Haven, New Haven Co., Connecticut, 16 October 1881; in Emerton Collection, MCZ, examined.

Description.—Total length: female 2.3-2.65 mm, male 2.2-2.3 mm. Carapace: length: female 1.1-1.25 mm, male 1.05-1.1 mm. Orange-red, suffused anteriorly with chestnut brown or black to give a striking contrast. In the male the carapace is elevated anteriorly, the form of the elevation being somewhat variable (Figs. 147, 148, 155); the elevation has a dense covering of trifurcate and simple hairs (Fig. 307), and there is a minor cleft in front, above the AM eyes. The pedicel (Fig. 167) is relatively long and sclerotized, and is conspicuous ventrally. Chelicerae: the lateral striae of the female are spaced more or less as in *W. directa*, while in the male they are more widely spaced than in *W. directa*. Abdomen: white or grey-white, darkened posteriorly around the spinners. Sternum: orange with dusky margins, dotted to a variable extent with small pits, each bearing a tiny hair. Legs: orange to yellow; rather slender, with tibia I 1/d 7.5-8 (female), 8-9 (male). TmI: female 0.47-0.52, male 0.50-0.52. Female palp: all segments are darker in color than the



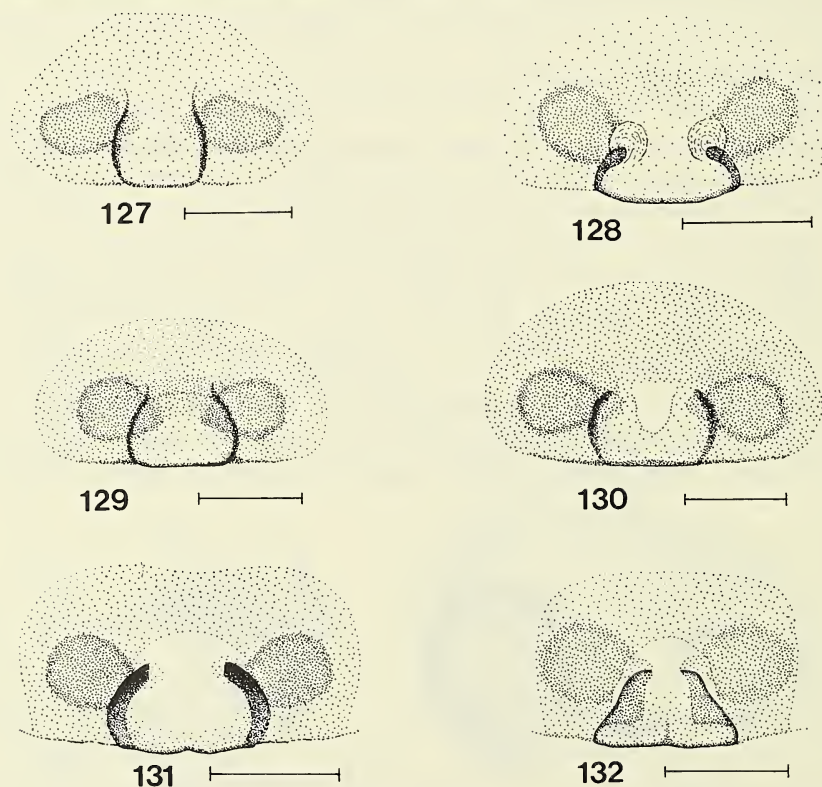
Figs. 125-126.—Male palps. 125, *W. vigilax*, ectal; 126, *W. vigilax*, mesal (Scale lines 0.1 mm).

legs. Male palp: Fig. 134; identical with that of *W. directa*. Epigynum: rather more convex than in *W. directa*, but otherwise not distinguishable.

Diagnosis.—The male of *W. pallida* is diagnosed by the form of the carapace (Figs. 147, 148) and the color. The carapace of *W. subpallida* (Fig. 149) is virtually indistinguishable from that of *W. pallida*, and the males of these two species can be distinguished only by the cheliceral file, which in *W. subpallida* is much more closely spaced than in *W. pallida*. The male of *W. carolina* has the carapace profile rather similar to that of *W. pallida* (Fig. 153 cf. Fig. 147), but the anterior elevation is higher; the cheliceral striae in *W. carolina* male are more widely spaced than in *W. pallida* male, and the membraneous part of the SA in *W. carolina* is shorter, as in *W. brevicornis* (Fig. 135). A further difference lies in the form of the pedicel, which is long and conspicuous in *W. pallida* male, but short and inconspicuous in *W. carolina*. The carapace of *W. prominens* male (Fig. 150) is also rather like that of *W. pallida*: for the separation of these two species, see *W. prominens* diagnosis. The female of *W. pallida* is grouped in the key with *W. subpallida*; these two species can be distinguished only by the cheliceral file, the striae of which are much more closely spaced in *W. subpallida* than in *W. pallida*.

Distribution.—All the records except one are in the eastern half of the continent (Map 13).

Natural History.—Females have been taken in every month except December, males in February, April-June and September-November. Habitats recorded are in woods, in soil and on low vegetation (by sweeping).



Figs. 127-132.—Epigyna. 127, *W. dixiana*; 128, *W. floridiana*; 129, *W. digitata*; 130, *W. maesta*; 131, *W. aurata*; 132, *W. puella* (Scale lines 0.1 mm).

Walckenaeria subpallida, new species

Figs. 149, 158; Map 12

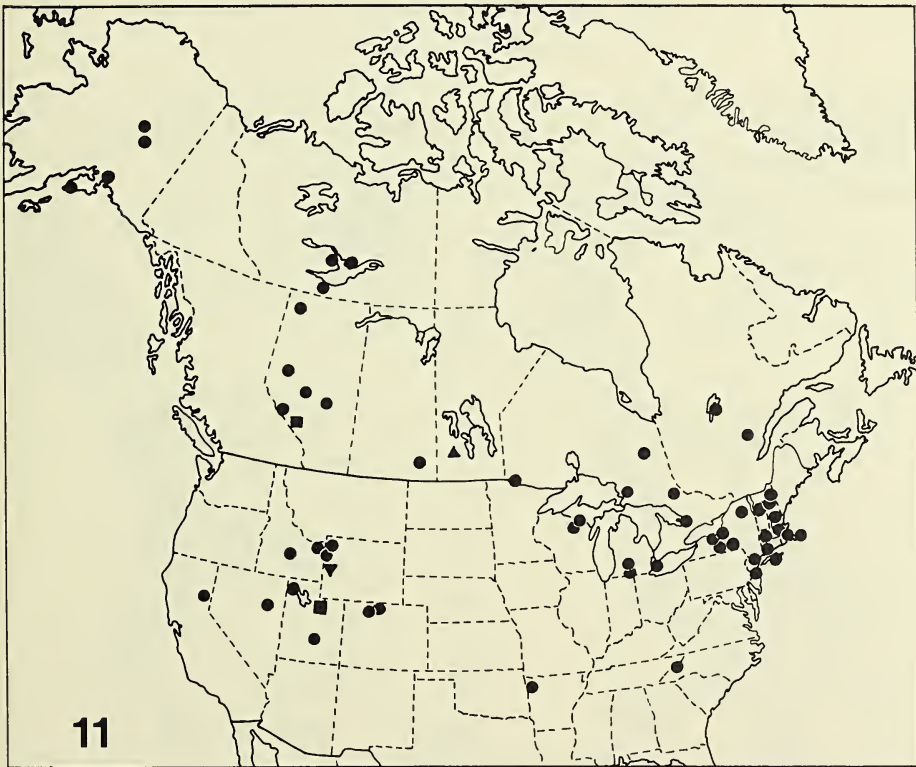
Type.—Male holotype from Neshaminy Creek, 2 miles northeast of Jamison, Pennsylvania, 22 May 1966 (J. and W. Ivie); deposited in AMNH.

Description.—Both sexes were taken together. The species is more or less identical in size, color and genitalia with *W. pallida*. Total length: female 2.5-2.6 mm, male 2.2 mm. Carapace: length: female 1.1-1.2 mm, male 1.05 mm. The anterior elevation in the male (Fig. 149) is sometimes more prominent than in *W. pallida*, and the cleft below the lobe (Fig. 158) is sometimes more pronounced. The pedicel is clearly exposed, as in *W. pallida*. Chelicerae: the lateral striae are closely spaced in both sexes, almost as close as in *W. subdirecta*. Male palp: segments suffused with dark brown or black; palpal organs identical with those of *W. directa*. Epigynum: not distinguishable from that of *W. pallida*.

Diagnosis.—This species is close to *W. pallida*, and its diagnosis is dealt with under that species.

Distribution.—Known only from a few localities in the eastern half of the continent (Map 12).

Natural History.—Adult females have been taken in April-June and October, males in March-June and October. Nothing was recorded on habitat.



Map 11.—North America. Distributions of *W. communis* (circles), *W. prominens* (triangle), *W. subvigilax* (inverted triangle) and *W. pullata* (squares).

Walckenaeria prominens, new species

Figs. 150, 156, 161; Map 11

Type.—Male holotype from near Wasagaming, Riding Mountain National Park, Manitoba, 29 August 1979 (J. and M. Redner); deposited in CNC.

Description.—Only the male is known; its relatively pale color may indicate that the specimen had only just completed its final molt. Total length: male 2.9 mm. Carapace: length: male 1.45 mm. The small lobe or horn (Fig. 156, 161) has a well-defined groove anteriorly, and is covered with numerous spatulate and simple hairs. Chelicerae: the lateral striae are moderately closely spaced. Abdomen: grey-black. Sternum: yellow, with dusky markings. Legs: pale yellow; stouter than in *W. pallida*, with tibia I 1/d ca 6. TmI: male 0.55-0.57. Male palp: indistinguishable from that of *W. directa*.

Diagnosis.—The male of *W. prominens* is diagnosed by the form of the carapace lobe (Figs. 150, 156, 161). From in front, this resembles the lobes of *W. pallida* (Fig. 155) and *W. subpallida* (Fig. 158), but the lateral view distinguishes *W. prominens*. *W. prominens* has a much less striking color than *W. pallida*, and the pedicel is not conspicuous. In addition, the legs of *W. prominens* are stouter than those of *W. pallida* and *W. subpallida*: *W. prominens* has tibia I 1/d 6, cf. 8.5-9 for *W. pallida/subpallida*.

Distribution.—Known only from the type locality (Map 11).

Natural History.—The male was taken in August, in moss in a boggy area.

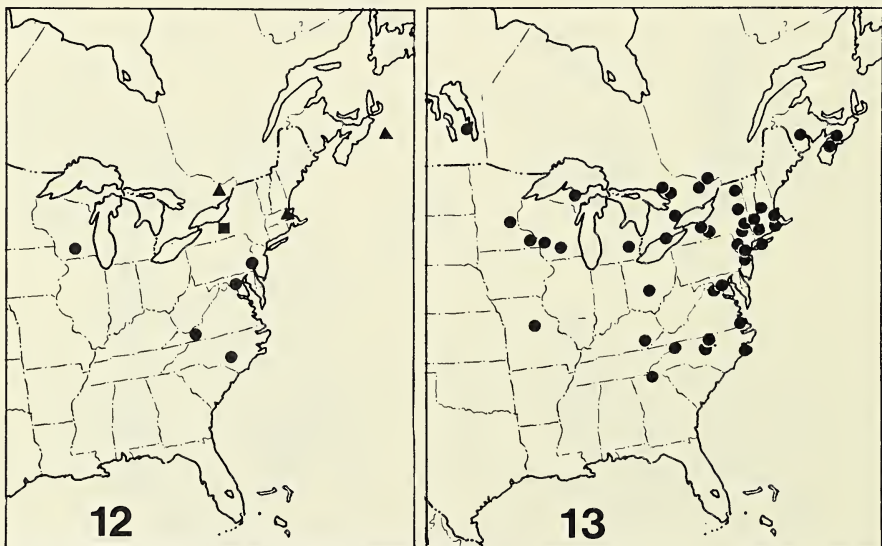
Walckenaeria indirecta (O.P.-Cambridge)

Figs. 141, 144; Map 12

Erigone indirecta O.P.-Cambridge 1874:440.

Cornicularia indirecta: Emerton 1882:41; Crosby and Bishop 1931:370; Roewer 1942:663; Kaston 1948:166; Bonnet 1956:1223.

Walckenaeria (Pseudoprosopotheca) indirecta: Wunderlich 1972:383.

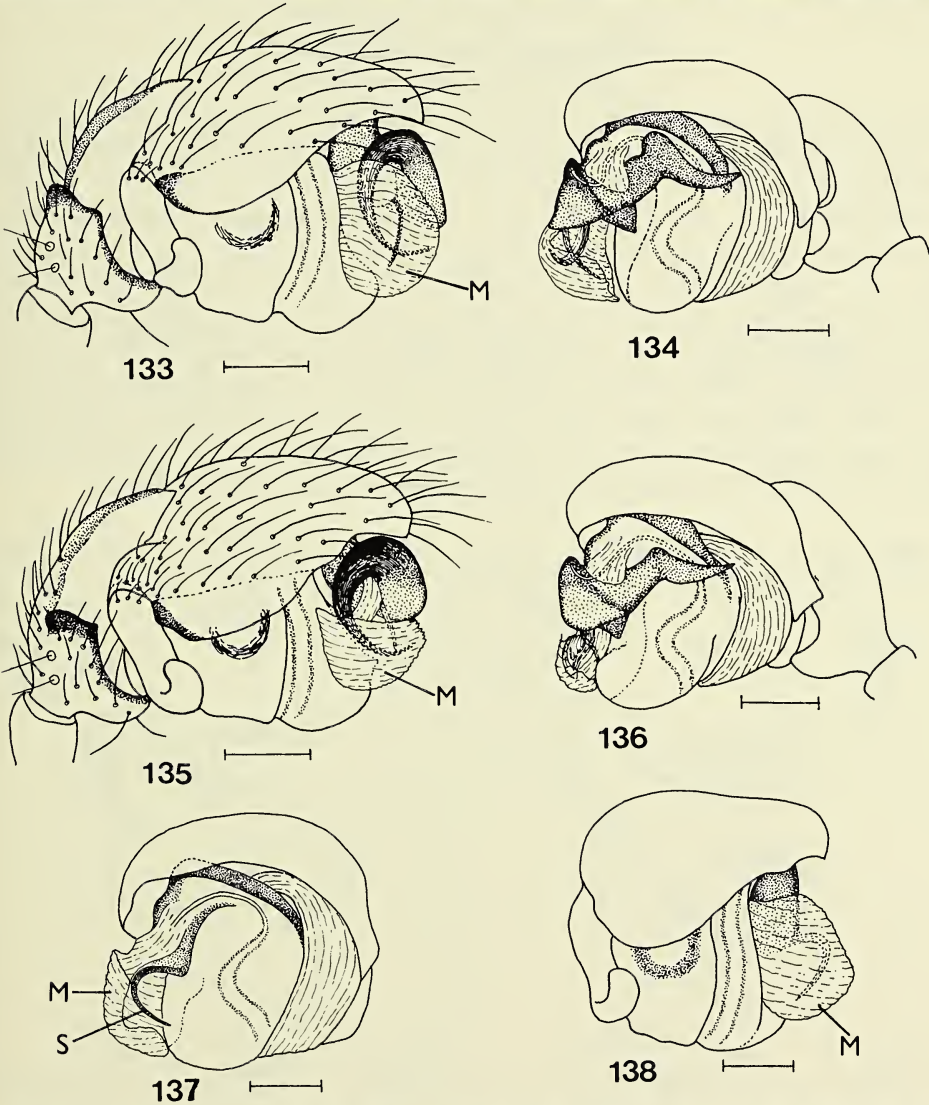


Map 12.—Eastern North America. Distribution of *W. subpallida* (circles), *W. indirecta* (triangles) and *W. breviarua* (square).

Map 13.—Eastern North America. Distribution of *W. pallida* (circles).

Type.—Male and female syntypes in Hope Entomological Collections, Oxford; examined. No type locality is given.

Description.—Total length: female 2.45–3.1 mm, male 2.8 mm. Carapace: length: female 1.0–1.15 mm, male 1.25 mm (excl. horn). Orange to chestnut brown, slightly to heavily darkened anteriorly in female, heavily darkened or black anteriorly in male. The carapace is long and narrow anteriorly, especially in the male. The spatulate hairs on the male horn (Figs. 141, 144) extend almost to the posterior median eyes, and the posterior row of eyes is strongly procurved. The pedicel is conspicuous ventrally, though perhaps rather less so than in *W. pallida* (Fig. 167). Chelicerae: the lateral striae are spaced more or less as in *W. directa* in the female, but rather more widely spaced in the male. Abdomen: grey. Sternum: orange, with dusky margins: a few minute pits are



Figs. 133–138.—Male palps. 133, *W. directa*, ectal; 134, *W. pallida*, mesal; 135, *W. brevicornis*, ectal; 136, *W. carolina*, mesal; 137, *W. directa*, mesal, ED removed; 138, *W. directa*, ectal, ED removed. Abbreviations: M, membranous part of SA; S, sickle-shaped end of SA (Scale lines 0.1 mm).

sometimes present. Legs: femora orange, remaining segments brown. TmI: female 0.60-0.70, male 0.60-0.62. Female palp: tibia and tarsus darkened. Male palp: not distinguishable from that of *W. directa*. Epigynum: not distinguishable from that of *W. directa*.

Diagnosis.—The male of *W. indirecta* is diagnosed by the form of the horn, the pro-curved posterior eyes and the long pedicel (see *W. directa* diagnosis). The female has a long pedicel as in *W. directa/subpallida*, and is separated from these species by the darker colored abdomen and the stouter legs.

Distribution.—*W. indirecta* appears to be a rare species; apart from the types, I have seen authentic specimens from three localities only in the north-east (Map 12).

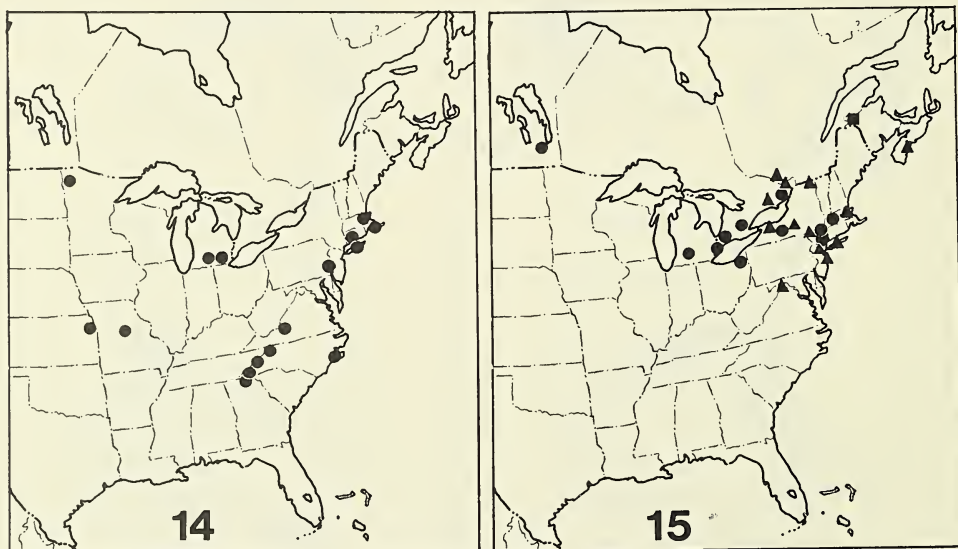
Natural History.—Adults of both sexes have been taken in May-June; the only locality recorded is in a sphagnum bog.

Walckenaeria oregona, new species

Figs. 154, 160, 163, 171; Map 10

Type.—Male holotype from Corvallis, Benton Co., Oregon, 7 March 1949 (V. Roth); deposited in AMNH.

Description.—The two sexes were taken together. Total length: female 2.8-3.0 mm, male 2.5-2.6 mm. Carapace: length: female 1.1-1.15 mm, male 1.2 mm. Orange, with faint dusky markings. Male carapace raised anteriorly into a small lobe with a distinct cleft beneath (Figs. 154, 160); the lobe has two longitudinal rows of spatulate hairs (Fig. 163). Chelicerae: lateral striae widely spaced in female, rather less widely spaced in male. Abdomen: grey to black. Sternum: orange to orange-brown. TmI: female 0.55-0.60, male 0.53-0.55. Female palp: tibia and tarsus darker than the legs. Male palp: palpal organs not distinguishable from those of *W. directa*, but the palpal tibia shows minor differences (Fig. 171 cf. Fig. 168). Epigynum: not distinguishable from that of *W. directa*.



Map 14.—Eastern North America. Distribution of *W. brevicornis* (circles).

Map 15.—Eastern North America. Distribution of *W. tibialis* (circles), *W. tumida* (triangles) and *W. teres* (square).

Diagnosis.—The male of *W. oregona* is diagnosed by the form of the male carapace (Figs. 154, 160); this bears some resemblance to that of *W. pallida*, but the cleft beneath the lobe is much more pronounced. The coloration of *W. oregona* is also quite different from that of *W. pallida*. The female of *W. oregona* is grouped in the key with *W. directa* and *W. subdirecta*; the separation of these three species is based on the spacing of the cheliceral striae (see *W. directa* diagnosis).

Distribution.—Recorded from Oregon and Washington only (Map 10).

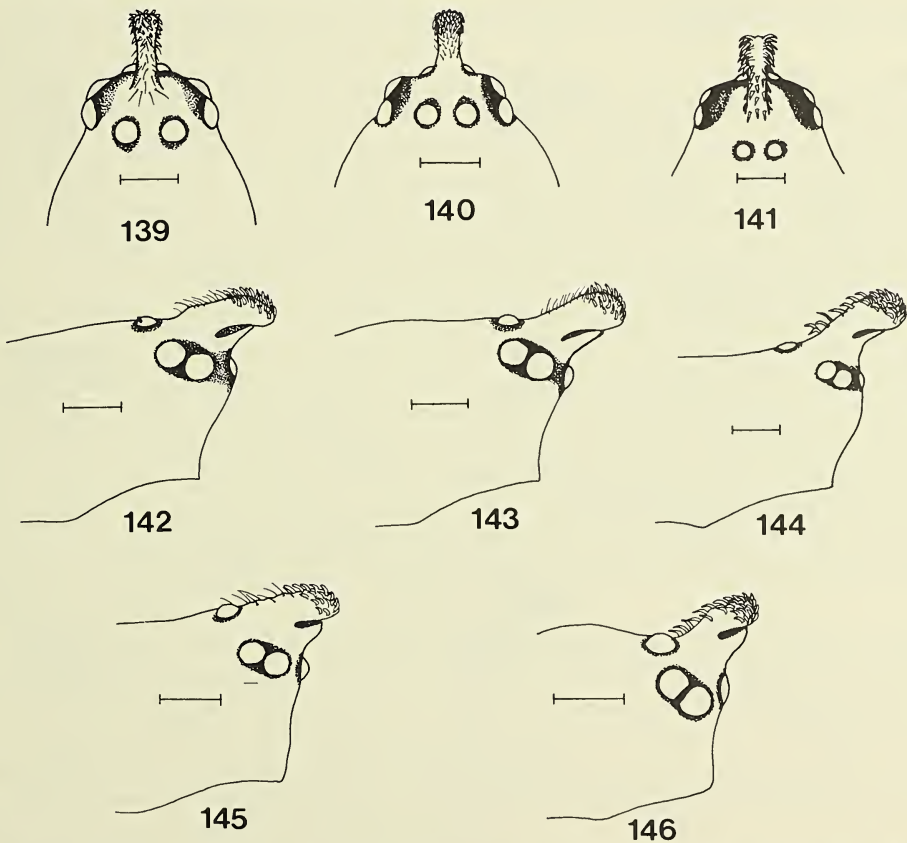
Natural History.—Adult females have been taken in all months except June, August and October, males in February, March, and September and November. The only habitat recorded was in fir needles.

Walckenaeria dondalei, new species

Figs. 151, 157, 162; Map 9

This species is named in honor of C. D. Dondale, who has been responsible for the capture of a number of the new *Walckenaeria* species described in this paper.

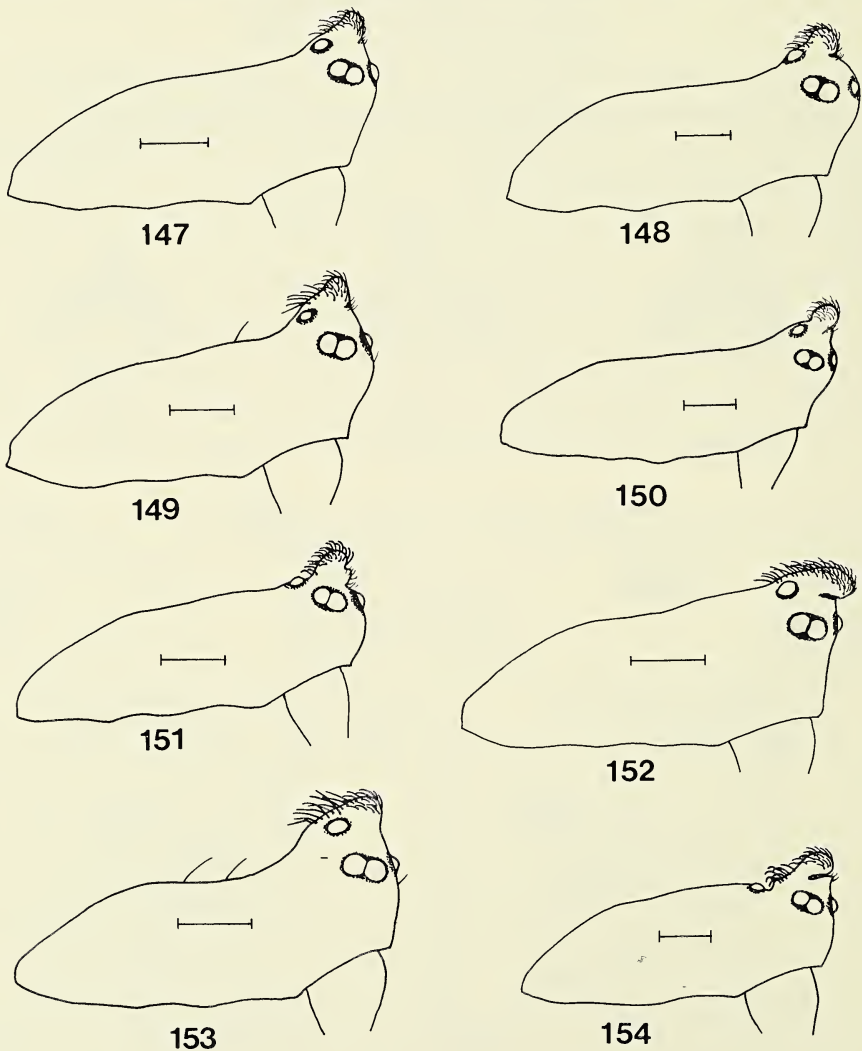
Type.—Male holotype from Chatterton, 13 miles north of Belleville, Ontario, 22 April 1969 (C. D. Dondale); deposited in CNC.



Figs. 139-146.—Male carapaces. 139, *W. directa*, dorsal; 140, *W. communis*, dorsal; 141, *W. indirecta*, dorsal; 142, *W. directa*, lateral; 143, *W. communis*, lateral; 144, *W. indirecta*, lateral; 145, *W. breviarua*, lateral; 146, *W. tibialis*, lateral (Scale lines 0.1 mm).

Description.—The female was taken at the type locality, but not with a male. Total length: female/male 2.2-2.55 mm. Carapace: length: female 1.0-1.05 mm, male 1.1-1.15 mm. Brown to deep chestnut brown, with dusky markings; lightly darkened anteriorly in female. The male carapace has a fairly large lobe (Figs. 151, 157, 162) which bears numerous spatulate hairs. Chelicerae: the lateral striae are moderately spaced in the female, approximately as in *W. directa*, and fairly closely spaced in the male. Abdomen: grey-black with faint paler markings. Sternum: orange, with blackish margins; a few tiny pits are sometimes present. Legs: yellow to orange. TmI: female 0.50-0.57, male 0.50-0.53. Male palp: the tibia and palpal organs are identical with those of *W. directa*. Epigynum: indistinguishable from that of *directa*.

Diagnosis.—The male of *W. dondalei* is diagnosed by the form of the carapace (Figs. 151, 162). Viewed laterally, the horn is fairly similar to those of *W. pallida*, *W. prominens*



Figs. 147-154.—Male carapaces, lateral. 147, *W. pallida*; 148, *W. pallida*, another specimen; 149, *W. subpallida*; 150, *W. prominens*; 151, *W. dondalei*; 152, *W. brevicornis*; 153, *W. carolina*; 154, *W. oregona* (Scale lines 0.2 mm).

and *W. oregona*; from in front, however, the horn is seen to be forked, which is not the case with these three species. (Fig. 162 cf. Figs. 155, 161, 163). The female of *W. dondalei* is grouped with *W. brevicornis* and *W. communis* in the key. *W. dondalei* female may be separable from *W. communis* by the darkening of the anterior leg segments in this latter species, and by the slightly different carapace profile, but these differences may be small (see *W. communis* diagnosis); distinction from *W. brevicornis* is possible only when the specimen of the latter species has the epigynum of the form shown in Fig. 176.

Distribution.—Known only from the type locality (Map 9).

Natural History.—Adult females were taken in May and October, males in September and October, in a meadow (pitfall).

Walckenaeria brevicornis (Emerton)

Figs. 135, 152, 165, 169, 176; Map 14

Cornicularia brevicornis Emerton 1882:42; Crosby and Bishop 1931:363; Roewer 1942:662; Kaston 1948:167; Bonnet 1956:1221.

Walckenaeria (Pseudoprosopotheca) brevicornis: Wunderlich 1972:383.

Type.—Male holotype from New Haven, New Haven Co., Connecticut, 14 November 1880; in Emerton Collection, MCZ, examined.

Description.—Total length: female 2.3-2.5 mm, male 2.15-2.25. Carapace: length: female/male 1.0-1.05 mm. Orange to chestnut brown, with faint dusky markings and margins; somewhat darkened anteriorly. The horn on the male carapace (Fig. 152) is short and blunt, with a clear fissure beneath, and clothed with the usual spatulate and simple hairs. Chelicerae: the lateral striae in the female are marginally more closely spaced than in *W. directa*, and in the male are spaced more or less as in *W. directa*. Abdomen: grey to black, sometimes paler anteriorly in the female; pale chevrons are sometimes visible, especially posteriorly. Sternum: shiny orange, with dusky margins. Legs: orange to pale orange. TmI: female 0.46-0.50, male 0.50-0.52. Female palp: tibia and tarsus usually darkened. Male palp: Figs. 135, 169; the membraneous sheet of the SA is smaller than in *W. directa*, covering less of the embolus on the ectal side (M, Fig. 135, cf. Fig. 133), and the lateral tibial apophysis is slightly shorter (Fig. 169 cf. Fig. 168). The anterior end of the ED is blunt, as in *W. carolina* (Fig. 136), not pointed, as in *W. pallida* (Fig. 134) and *W. directa*. Epigynum: Fig. 176; not all specimens have the convergent dark lines extending from the posterior area so clearly marked, and in such cases the epigynum is indistinguishable with certainty from that of *W. directa* (Fig. 175) and other species in this group.

Diagnosis.—The male of *W. brevicornis* is diagnosed by the form of the horn (Fig. 152), which is short and blunt. The horn is somewhat similar to that of *W. breviaria*: see *W. breviaria* diagnosis. The female of *W. brevicornis* is grouped with *W. communis* and *W. dondalei* in the key, and separation of the females of these three species is often unreliable: see *W. communis* and *W. dondalei* diagnoses.

Distribution.—*W. brevicornis* seems to be limited to the eastern part of the continent (Map 14). It has not been recorded from Canada.

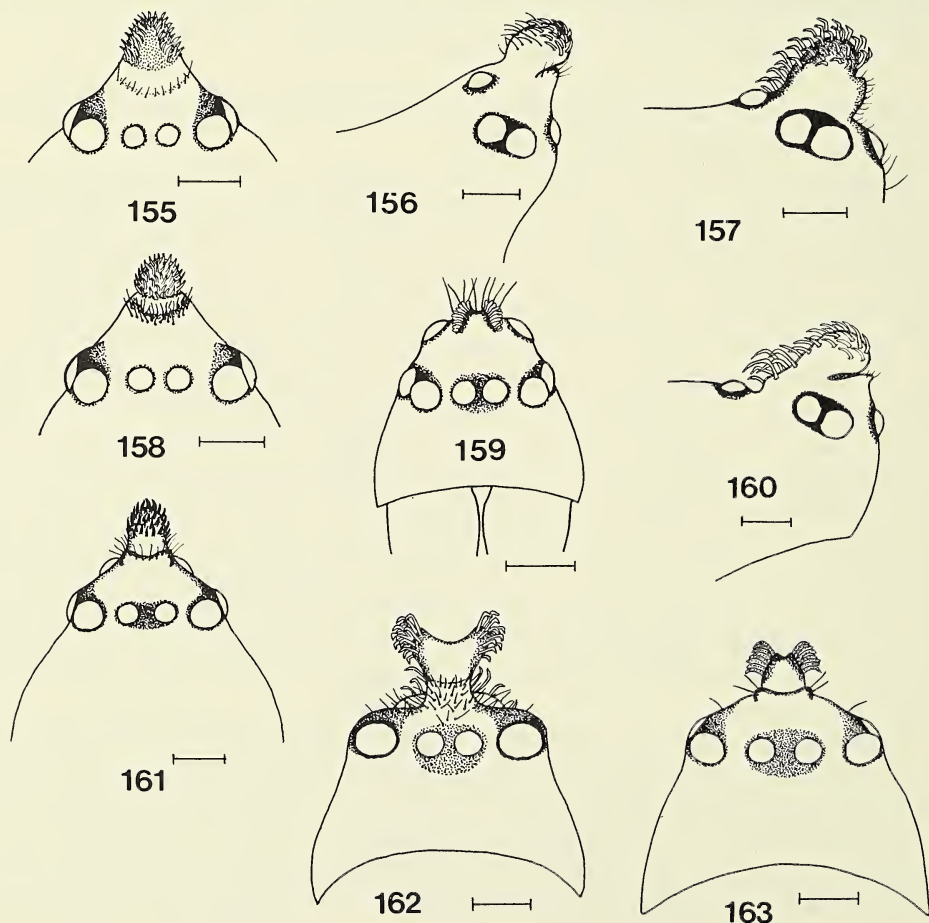
Natural History.—Adult females have been taken in April-June and September-November, males in January-May and October-November. Nothing is recorded on habitat. Both sexes were taken in September, on a fence, presumably about to aeronaut.

Walckenaeria carolina, new species

Figs. 136, 153, 159, 166, 170, 177; Map 10

Type.—Male holotype from Duke Forest, Durham Co., North Carolina, 6 February 1964, at 1500 ft. (J. W. Berry); deposited in MCZ.

Description.—Both sexes have been taken at the type locality, but at different times. Total length: female 2.4-2.9 mm, male 2.2-2.35 mm. Carapace: length: female 1.1 mm, male 1.0 mm. Glossy orange-red to chestnut brown, with blackish margins; not significantly darkened anteriorly. The carapace is raised anteriorly in the female (Fig. 166), and more so in the male (Figs. 153, 159); the elevation in the male is clothed with the usual spatulate and simple hairs. Chelicerae: the lateral striae are more widely spaced than in *W. pallida* in both sexes. Abdomen: grey. Sternum: shiny orange, with blackish margins. Legs: orange to yellow. TmI: female 0.51-0.57, male 0.50. Male palp: Figs. 136, 170. The ED is not pointed anteriorly, and the membranous sheet of the SA is short like that of *W. brevicornis* (Fig. 135); the palpal tibia has the long apophysis rather shorter than in *W. brevicornis* (Fig. 170 cf. Fig. 169). Epigynum: Fig. 177. Although the carapace of this



Figs. 155-163.—Male carapaces. 155, *W. pallida*, in front; 156, *W. prominens*, lateral; 157, *W. dondalei*, lateral; 158, *W. subpallida*, in front; 159, *W. carolina*, in front; 160, *W. oregona*, lateral; 161, *W. prominens*, in front; 162, *W. dondalei*, in front; 163, *W. oregona*, in front (Scale lines 0.1 mm).

species is reminiscent of *W. pallida*, the form of the male palp shows that it is more closely related to *W. brevicornis*.

Diagnosis.—The male of *W. carolina* is diagnosed by the form of the carapace (Fig. 153), and is dealt with under *W. pallida* diagnosis. The female is grouped with *W. directa*, *W. subdirecta* and *W. oregona* in the key; it is readily separated from these species by the epigynum (Fig. 177), and by the more sharply raised carapace (Fig. 166).

Distribution.—Known only from a few mid-eastern areas of the continent (Map 10).

Natural History.—Adult females have been taken in April, May and October, males in February and October. The type was taken in young pines (pitfall) at ca. 450 m.

tibialis Group

This group contains only three species, and diagnosis is relatively easy on the basis of the male palpal tibiae and the female epigyna.

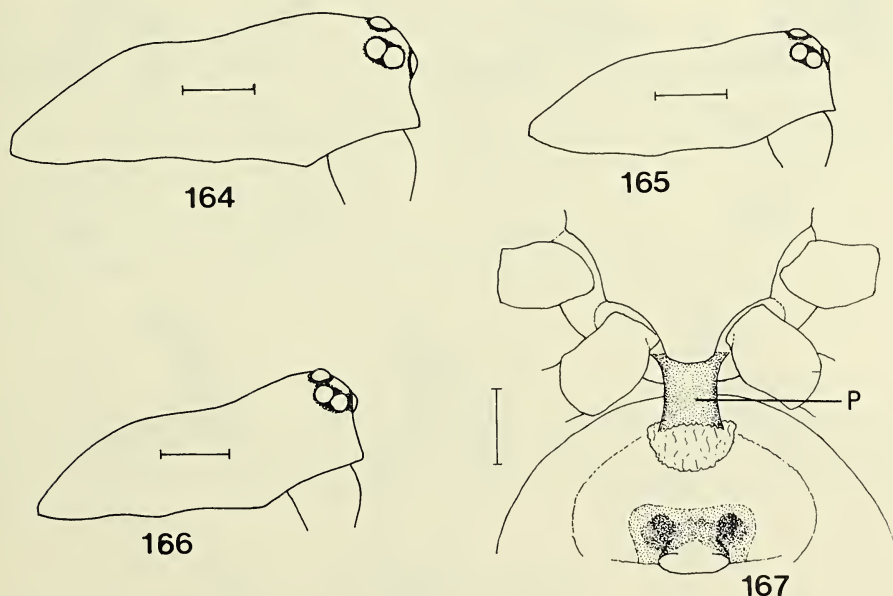
Walckenaeria tibialis (Emerton)

Figs. 146, 172, 179, 182, 184; Map 15

Cornicularia tibialis Emerton 1882:41; Crosby and Bishop 1931:373; Roewer 1942:664; Kaston 1948:167; Bonnet 1956:1225.

Walckenaeria (Pseudoprosopotheca) tibialis: Wunderlich 1972:383.

Type.—Male and female syntypes from Mt. Tom, Hampshire Co., near Holyoke, Hampden Co., Massachusetts, 4 April 1878; in Emerton Collection, MCZ, examined.



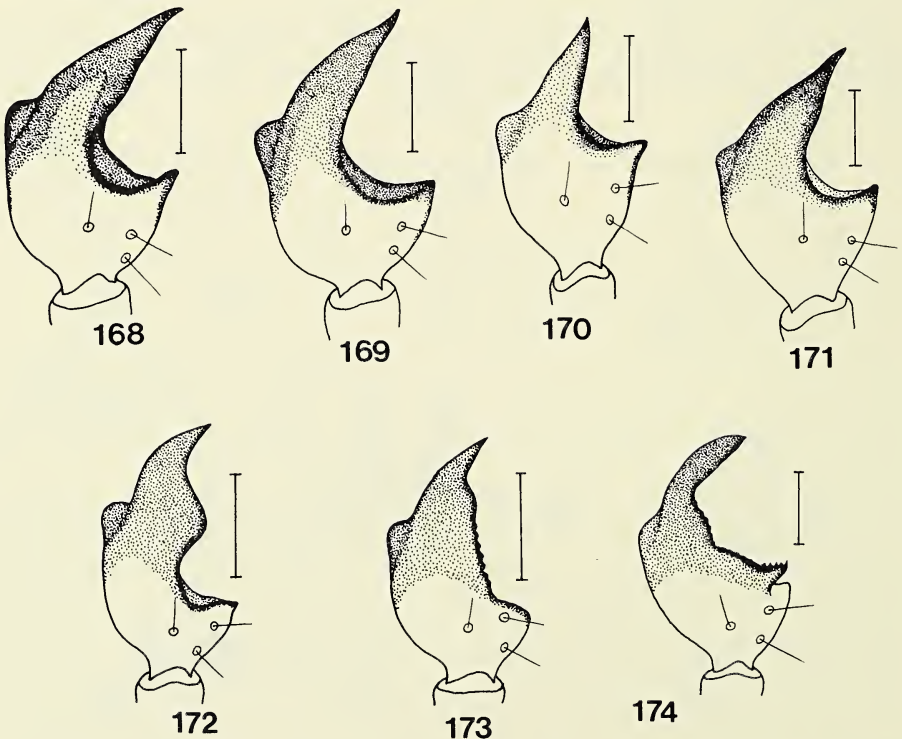
Figs. 164-167.—164, *W. communis*, female carapace, lateral; 165, *W. brevicornis*, female carapace, lateral; 166, *W. carolina*, female carapace, lateral; 167, *W. pallida*, female, pedicel. Abbreviation: P, pedicel (Scale lines 0.2 mm).

Description.—Total length: female 1.9 mm, male 1.8-1.9 mm. Carapace: length: female 0.85-0.90, male 0.80-0.90 (excl. horn). Deep chestnut brown. The male has a stout horn anteriorly (Fig. 146); the length of the horn is somewhat variable. There is a clump of stout spatulate hairs between the base of the horn and the posterior eyes. Lines of minute pits radiating from the fovea are sometimes visible in the male. Chelicerae: the lateral striae are fairly widely spaced in both sexes. Abdomen: black. Sternum: orange to deep brown, with blackish margins; the surface is marked with numerous tiny pits. Legs: orange to deep brown. TmI: female 0.40, male 0.38-0.42. Male palp: Figs. 172, 182, 184. Epigynum: Fig. 179.

Diagnosis.—*W. tibialis* male is diagnosed by the carapace horn (Fig. 146), which is of the same type as in *W. directa* but shorter and more erect, coupled with the form of the palp, particularly of the SA (Figs. 182, 184) and of the palpal tibia (Fig. 172). *W. tumida* and *W. teres* have the carapace horn and the palpal organs more or less identical with those of *W. tibialis*, but are readily distinguished by the forms of the palpal tibiae (Figs. 173, 183: 174, 185 cf. 172, 182). *W. tibialis* female is diagnosed by the epigynum (Fig. 179); this is very like that of *W. tumida* (Fig. 180), but the spermathecae are rather smaller and set less far forwards.

Distribution.—Most of the records are from the northeastern states of U.S.A. and from Ontario, but there is one record from Manitoba (Map 15).

Natural History.—Adult females have been taken in April and July, males in April, May and December. Habitats recorded are in a cornfield, at the edge of moist woods and under a rock.



Figs. 168-174.—Male palpal tibiae, dorsal. 168, *W. directa*; 169, *W. brevicornis*; 170, *W. carolina*; 171, *W. oregona*; 172, *W. tibialis*; 173, *W. tumida*; 174, *W. teres* (Scale lines 0.1 mm).

Walckenaeria tumida (Crosby and Bishop)

Figs. 173, 180, 181, 183; Map 15

Cornicularia tumida Crosby and Bishop 1931:374; Roewer 1942:664; Bonnet 1956:1225.

Walckenaeria (Pseudoprosopotheca) tumida: Wunderlich 1972:383.

Type.—The male holotype (Little Pond, Orange Co., New York, 25 May 1920) cannot be found in AMNH; there is however one male, determined by Crosby and Bishop, in the AMNH collection.

Description.—Total length: female 1.55 mm, male 1.40-1.55 mm. Carapace: length: female 0.7 mm, male 0.65-0.7 mm. Brown to deep brown. The male horn is as in *W. tibialis*. Chelicerae: the lateral striae are fairly widely spaced in both sexes. Abdomen: grey. Sternum: brown, with blackish margins; pitted to a smaller extent than in *W. tibialis*. Legs: orange-brown. TmI: female 0.40, male 0.40-0.45. Male palp: Figs. 173, 183. Epigynum: Fig. 180; the epigynum is very small, and the full detail of the internal genitalia (Fig. 181) could not be seen.

Diagnosis.—See *W. tibialis* diagnosis.

Distribution.—This is very similar to that of *W. tibialis* (Map 15)

Natural History.—Adult females have been taken in April-August and in October, males in March-June, September and “winter/spring”. Habitats recorded are in sphagnum bog, in sphagnum fen and in an oak stand.

Walckenaeria teres, new species

Figs. 174, 185; Map 15

Type.—Male holotype from Green River, 30 miles north of Edmunston, New Brunswick, 6 June 1961 (T. R. Renault); deposited in CNC.

Description.—Only the male is known. Total length: male 2.0-2.1 mm. Carapace: length: male 0.90-1.0 mm. Chestnut brown with dusky markings. The male horn is as in *W. tibialis*. Chelicerae: the lateral striae are moderately widely spaced. Abdomen: grey-black. Sternum: orange, with margins dusky; the surface is marked with numerous small pits. Legs: orange brown. TmI: male 0.50. Male palp: Figs. 174, 185.

Diagnosis.—See *W. tibialis* diagnosis.

Distribution.—Known only from the type locality (Map 15).

Natural History.—The adult males were taken in June, by beating.

tricornis Group

The males of this group have closely similar palpal organs, but can be diagnosed by the form of the palpal tibiae. The females of several of the species have virtually identical epigyna, and, unless the female is taken with a male, diagnosis to species level is sometimes impossible.

Partial keys to species

Males

1. Palpal tibia as Figs. 194, 195, with lateral bulge.
 *tricornis*, *palustris* (see species descriptions)
 Palpal tibia with a distinct lateral apophysis 2

2. Lateral apophysis small (Figs. 196, 197)3
 Lateral apophysis larger (Figs. 198-202).4
3. Lateral apophysis narrow (Fig. 196); carapace lobe constricted (Fig. 189)
 *bifida*
 Lateral apophysis broad (Fig. 197); carapace lobe scarcely constricted. *serrata*
4. Carapace lobe distinctly constricted (Fig. 191)*occidentalis*
 Carapace lobe scarcely constricted (Fig. 192)
 *helenae, reclusa, septentrionalis, columbia* (see species descriptions)

Females

1. Epigynum as Figs. 203, 204, 206-208
 *palustris, aprilis, solivaga, anceps* (see species descriptions)
 Epigynum as Figs. 209-211
 *weber, occidentalis, helenae, reclusa, septentrionalis, columbia* (see species descriptions)

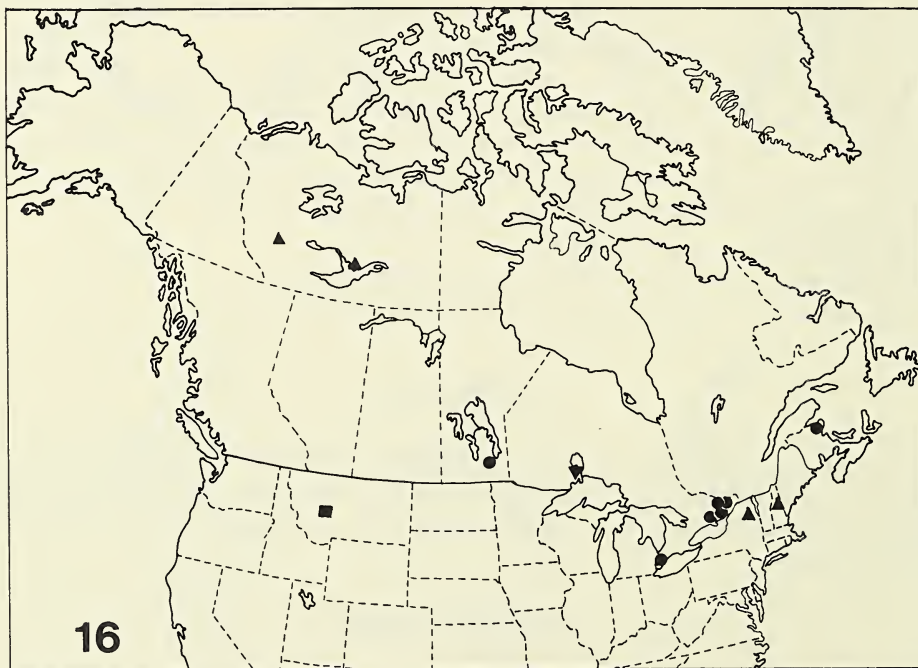
Walckenaeria tricornis (Emerton)

Figs. 186, 190, 194; Map 16

Cornicularia tricornis Emerton 1882:43.

Tigellinus tricornis: Crosby and Bishop 1931:377; Roewer 1942:667; Bonnet 1959:4621.

Walckenaeria (Pseudotigellinus) tricornis: Wunderlich 1972:391.



Map 16.—North America. Distributions of *W. palustris* (circles), *W. tricornis* (triangles), *W. anceps* (inverted triangle) and *W. helenae* (square).

Type.—Male holotype from Mt. Washington, Coos Co., New Hampshire, 10 June 1877; in Emerton Collection, MCZ, examined.

Description.—Only the male is known. Total length: male 1.5-1.75 mm. Carapace: length: male 0.70-0.75 mm. Orange to deep brown, with dusky markings; the lobe is well constricted behind the anterior fork (Fig. 190). Chelicerae: lateral striae fairly closely spaced. Abdomen: grey to black. Sternum: orange to brown. Legs: orange to brown. TmI: male 0.39-0.41. Male palp: Figs. 186, 194; the tibia and tarsus are dark in color.

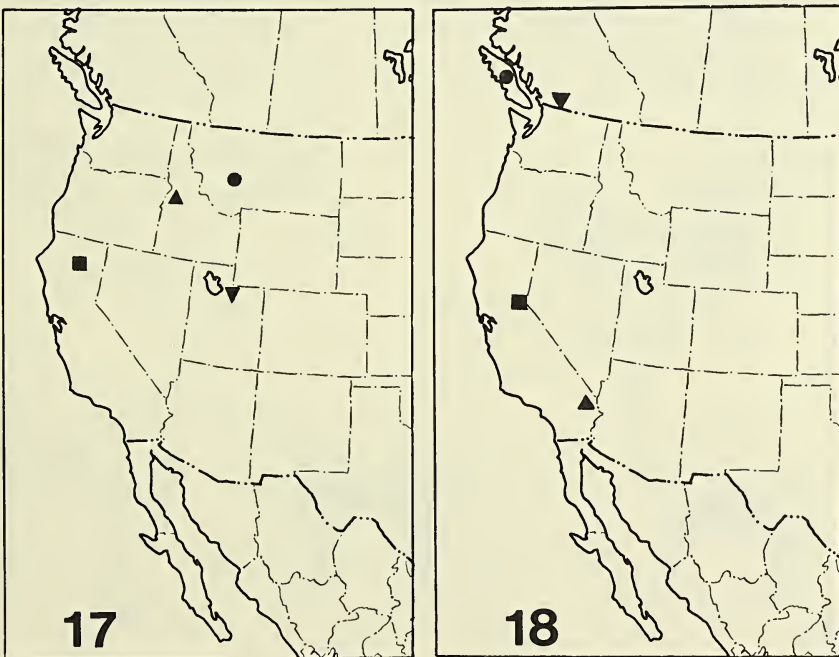
Diagnosis.—The male of *W. tricornis* is diagnosed by the form of the palpal tibia (Fig. 194) and the palpal organs (Fig. 186), coupled with the form of the carapace lobe (Fig. 190). The palpal tibia is of the same pattern as that of *W. palustris* (Fig. 195), but this species has the tibia wider in the mid-section and less indented; in addition, the lobe of *W. palustris* is narrower anteriorly than that of *W. tricornis* (Fig. 193 cf. Fig. 190). *W. tricornis* seems to be the only species in this group which has a barb-shaped termination to the embolus (Fig. 186).

Distribution.—*W. tricornis* is recorded from high ground in the northeastern U.S.A. and from Northwest Territories (Map 16).

Natural History.—Adult males have been taken in June and August. The only locality recorded is in moss.

Walckenaeria palustris, new species
Figs. 193, 195, 203, 205, 206; Map 16

Type.—Male holotype from Mer Bleue, east of Ottawa, Ontario, 14 May-9 June 1975 (Dondale and Redner); deposited in CNC.



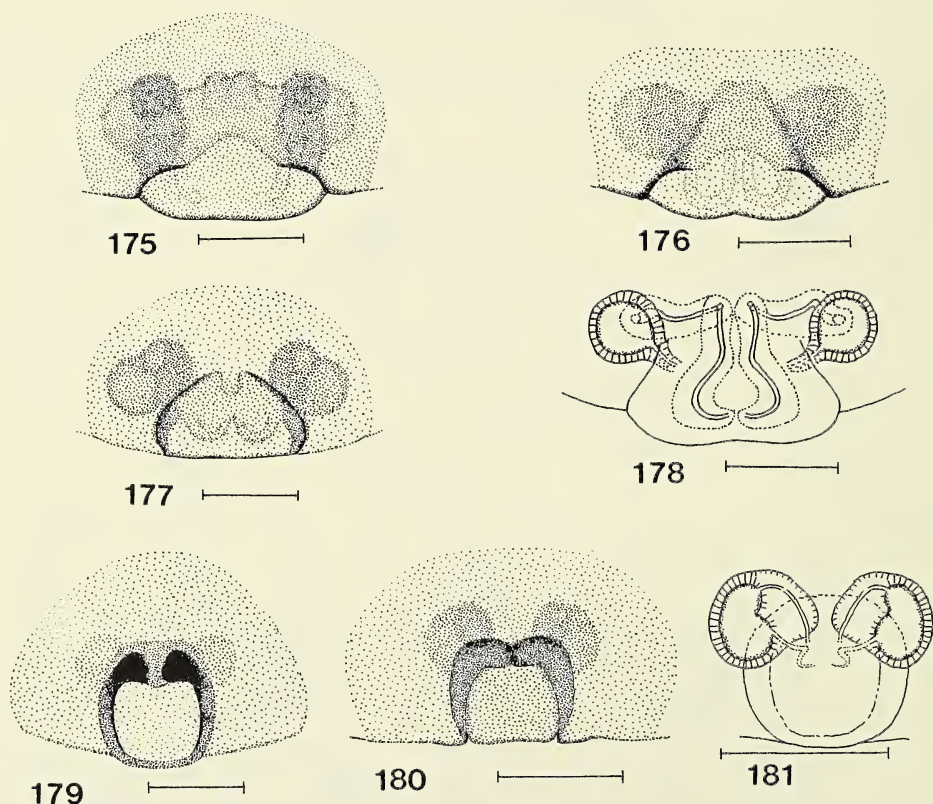
Map 17.—Western North America. Distributions of *W. solivaga* (circle), *W. reclusa* (triangle), *W. weber* (inverted triangle) and *W. serrata* (square).

Map 18.—Western North America. Distributions of *W. septentrionalis* (circle), *W. occidentalis* (triangle), *W. columbia* (inverted triangle) and *W. bifida* (square).

Description.—Both sexes have been taken together. Total length: female 1.55-1.75 mm, male 1.45-1.55 mm. Carapace: length: female 0.60-0.65 mm, male 0.55-0.65 mm. Brown, with dusky markings and margins. The male lobe (Fig. 193) is constricted behind the fork. Chelicerae: lateral striae closely spaced in both sexes. Abdomen: grey-black. Sternum: yellow-brown, with dusky margins. Legs: brown to orange-brown. TmI: female/male 0.40-0.43. Male palp: Fig. 195. Epigynum: Figs. 203, 205, 206. The width and shape of the central area shows some variation; the female from Manitoba, which I take to be this species, has the central area narrower than in the specimens from Ontario.

Diagnosis.—The male is diagnosed by the form of the palpal tibia (Fig. 195) and of the carapace lobe (Fig. 193); this species is close to *W. tricornis*, and the features distinguishing the males of these two species are dealt with under *W. tricornis* diagnosis. The female of *W. palustris* is diagnosed by the epigynum (Figs. 203, 206); this is generally similar to those of *W. aprilis* (Fig. 204), *W. solivaga* (Fig. 207) and *W. anceps* (Fig. 208), but the epigyna of the two latter species are sufficiently different from that of *W. palustris* to make confusion unlikely. *W. palustris* is distinguished from *W. aprilis* by the larger size of the epigynum and closer spacing of the cheliceral striae in the latter species, and by the proportions of the legs (MTI/tI in *W. palustris* ca. 1.15, in *W. aprilis* ca. 1.4); the geographical distribution should also be taken into consideration.

Distribution.—The species is known only from southern Canada (Map 16).



Figs. 175-181.—Epigyna, ventral. 175, *W. directa*; 176, *W. brevicornis*; 177, *W. carolina*; 178, *W. directa*, internal genitalia, cleared; 179, *W. tibialis*; 180, *W. tumida*; 181, *W. tumida*, internal genitalia, cleared (Scale lines 0.1 mm).

Natural History.—Adults of both sexes have been taken in May-July. Habitats recorded are sphagnum bog, meadow, prairie grass, and amongst pines on sand dunes.

Walckenaeria aprilis, new species

Fig. 204; Map 19

Type.—Female holotype from 3 miles west of Forest, Scott Co., Mississippi, 11 April 1963 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Only the female is known. Total length: female 1.4 mm. Carapace: length: female 0.65 mm. Orange, with dusky margins. Chelicerae: lateral striae very closely spaced. Abdomen: black. Sternum: orange-yellow, with blackish margins. Legs: orange. TmI: female 0.38. Epigynum: Fig. 204.

Diagnosis.—*W. aprilis* female is diagnosed by the epigynum (Fig. 204); this is of the same general form as in *W. palustris* (Fig. 203), *W. solivaga* (Fig. 207) and *W. anceps* (Fig. 208). From the two latter species, *W. aprilis* is distinguished by the shape of the epigynum; the separation from *W. palustris* is dealt with under that species.

Distribution.—Known only from the type locality (Map 19).

Natural history.—The female was taken adult in April; nothing was recorded on habitat.

Walckenaeria solivaga, new species

Fig. 207; Map 17

Type.—Female holotype from Last Chance Gulch, Helena, Lewis and Clark Co., Montana, 3 October 1964 (J. and W. Ivie); deposited in AMNH.

Description.—Only the female is known. Total length: female 2.2 mm. Carapace: length: female 0.85 mm. Orange, with faint dusky markings and margins. Chelicerae:



Map 19.—North America. Distributions of *W. minuta* (circles), *W. tenella* (triangles) and *W. aprilis* (inverted triangle).

lateral striae moderately spaced. Abdomen: grey. Sternum: orange, with dusky margins. Legs: orange. TmI: female 0.42-0.45 mm. Epigynum: Fig. 207. This species may possibly be *Tigellinus perditus* Chamberlin (1948), but in the absence of any specimens of Chamberlin's species it is impossible to come to any valid conclusion on this possibility.

Diagnosis.—*W. solivaga* female is diagnosed by the epigynum (Fig. 207); in the single specimen known, this epigynum is distinguishable from those of *W. palustris* (Fig. 203) and *W. aprilis* (Fig. 204), but that of *W. anceps* (Fig. 208) is closely similar. *W. solivaga* and *W. anceps* are separable by the significantly smaller size of *W. anceps*, and by the proportions of the legs (MTI/tI in *W. solivaga* is 1.35, in *W. anceps* is 1.1).

Distribution.—Known only from the type locality (Map 17).

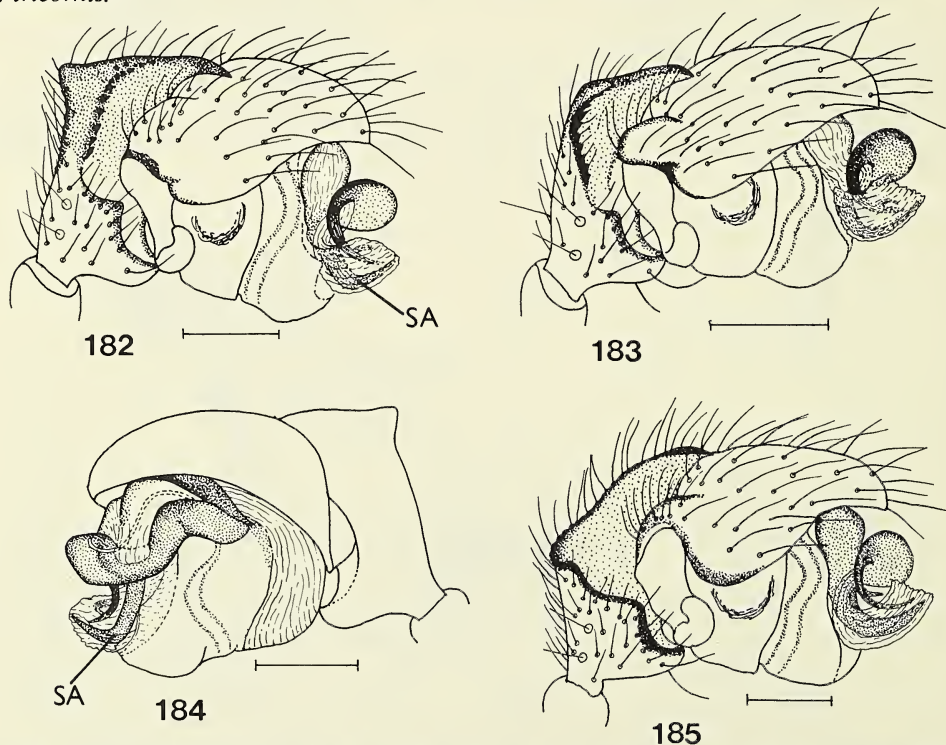
Natural History.—The female was taken adult in October; nothing was recorded on habitat.

Walckenaeria anceps, new species

Fig. 208; Map 16

Type.—Female holotype from 17 miles north of Black Sturgeon Lake, Ontario, 13 August 1972 (E. Lindquist); deposited in CNC.

Description.—Only the female is known. Total length: female 1.65 mm. Carapace: length: female 0.70 mm. Orange, with faint dusky markings. Chelicerae: lateral striae closely spaced. Abdomen: grey. Sternum: orange, with dusky margins. Legs: pale orange. TmI: female 0.40. Epigynum: Fig. 208. It is possible that this is the unknown female of *W. tricornis*.



Figs. 182-185.—Male palps. 182. *W. tibialis*, ectal; 183, *W. tumida*, ectal; 184, *W. tibialis*, mesal; 185, *W. teres*, ectal. Abbreviation: SA, suprategular apophysis (Scale lines 0.1 mm).

Diagnosis.—*W. anceps* female is diagnosed by the epigynum (Fig. 208), which has a wide central area covered by an integument of glassy appearance. *W. solivaga* has the epigynum (Fig. 207) very similar to that of *W. anceps*, though relatively not quite so broad: see *W. solivaga* diagnosis.

Distribution.—Known only from the type locality (Map 16).

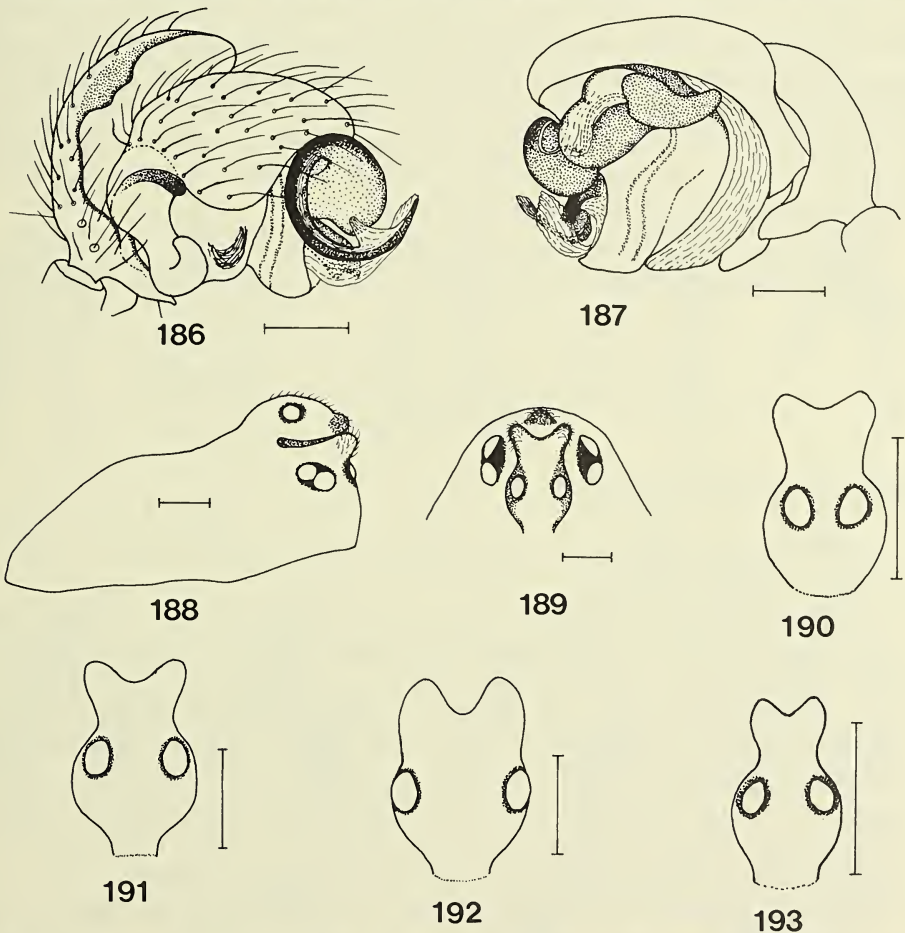
Natural History.—The female was taken adult in August, in conifer litter and moss.

Walckenaeria bifida, new species

Figs. 188, 189, 196; Map 18

Type.—Male holotype from Johnsville, Plumas Co., California, 25 October 1959 (J. S. Buckett); deposited in AMNH.

Description.—Only the male is known. Total length: male 1.60 mm. Carapace: length: male 0.70 mm. Orange-brown. The lobe (Fig. 188) is constricted in front of the eyes (Fig. 189). Chelicerae: the lateral striae are fairly closely spaced. Abdomen: black. Sternum:



Figs. 186-193.—186, *W. tricornis*, male palp, ectal; 187, *W. reclusa*, male palp, mesal; 188, *W. bifida*, male carapace, lateral; 189, *W. bifida*, male carapace, dorsal; 190, *W. tricornis*, male lobe, dorsal; 191, *W. occidentalis*, male lobe, dorsal; 192, *W. reclusa*, male lobe, dorsal; 193, *W. palustris*, male lobe, dorsal (Scale lines 0.1 mm).

orange, with dusky margins. Legs: orange. TmI: male 0.48. Male palp: Fig. 196; the lateral tibial apophysis is tiny and bifid at the tip.

Diagnosis.—The male of *W. bifida* is diagnosed by the form of the palpal tibia (Fig. 196); the lateral tibial apophysis is significantly smaller and narrower than in the other species in the *tricornis* group.

Distribution.—Known only from the type locality (Map 18).

Natural History.—The type male was adult in October; nothing was recorded on habitat.

Walckenaeria serrata, new species

Fig. 197; Map 17

Type.—Male holotype from 3 miles ENE of Manzanita Lake, Shasta Co., California, 16 September 1965 (J. and W. Ivie); deposited in AMNH.

Description.—Only the male is known. Total length: male 2.05 mm. Carapace: length: male 0.80 mm. Orange, with dusky markings and margins. The lobe is broad and not much constricted (as Fig. 192). Chelicerae: the lateral striae are moderately closely spaced. Abdomen: black. Sternum: orange, with dusky margins. Legs: orange. TmI: male 0.40. Male palp: Fig. 197.

Diagnosis.—*W. serrata* male is diagnosed by the palpal tibia (Fig. 197). The lateral apophysis is short and broad, weakly serrated on its margin; no other species in the *tricornis* group has the tibial apophysis of this form.

Distribution.—Known only from the type locality (Map 17).

Natural History.—The type male was adult in September; nothing was recorded on habitat.

Walckenaeria weber, (Chamberlin), new combination

Fig. 210; Map 17

Tigellinus weber Chamberlin 1948:557.

Type.—Female holotype from Smith and Morehouse Canyon, Utah, 7 October 1932 (W. Ivie); in AMNH, examined.

Description.—Only the female is known. Total length: female 2.2-2.4 mm. Carapace: length: female 0.90-0.95 mm. Orange, with dusky markings. Chelicerae: lateral striae fairly widely spaced. Abdomen: black. Sternum: chestnut brown. Legs: orange. TmI: female 0.40-0.45. Epigynum: Fig. 210. The females of *W. occidentalis*, *W. reclusa*, *W. septentrionalis*, *W. columbia* and *W. helenae* have epigyna which are indistinguishable or barely distinguishable from that of *W. weber*, and it cannot be ruled out that one of these species is *W. weber* (*W. helenae* and *W. reclusa* are most likely, from the geographical distributions). In order to establish the true identity of *W. weber* it will be necessary to capture a male and female together at, or very near to, the type locality.

Diagnosis.—Because of the close similarity to the epigynum of *W. weber* to those of the species mentioned above, the diagnosis of *W. weber* must for the present be regarded as very uncertain. Only specimens having the correct form of epigynum (Fig. 210), which were taken at or very near to the type locality, can be regarded as likely to belong to this species..

Distribution.—Known only from the type locality (Map 17).

Natural History.—Adult females were taken in June and October; nothing was recorded on habitat.

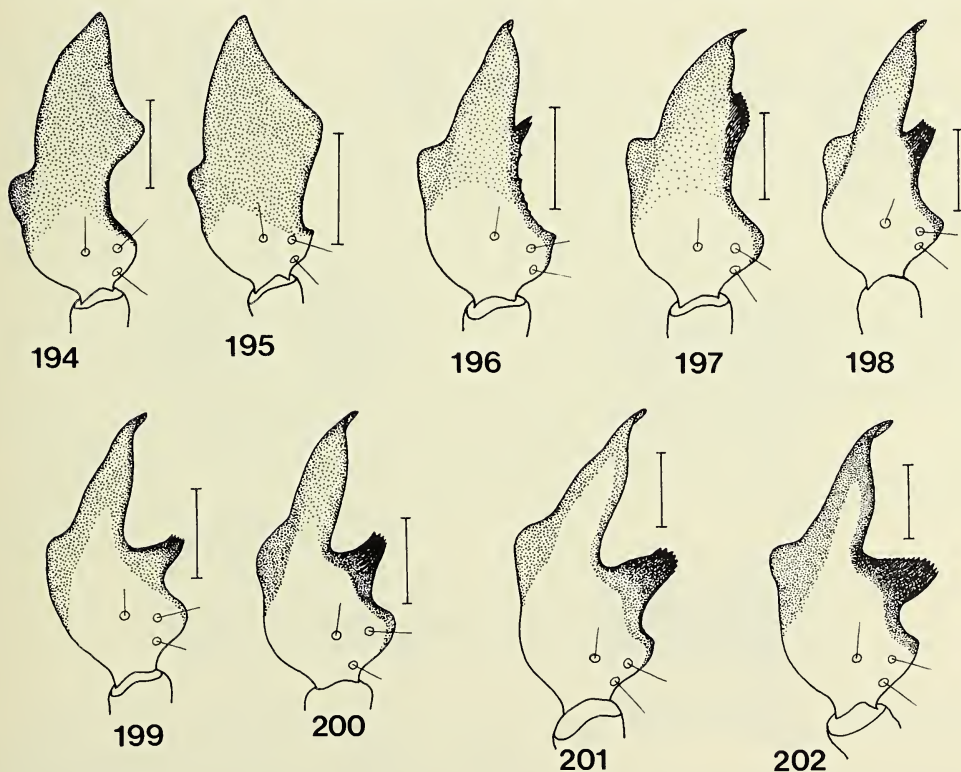
Walckenaeria occidentalis, new species

Figs. 191, 199, 209; Map 18

Type.—Male holotype from 1.8 miles below Jenks Lake, S. Bernadino Co., California, 23 March 1958 (I. Newell); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 2.4 mm, male 1.95 mm. Carapace: length: female 0.95 mm, male 0.75 mm. Orange brown, with dusky markings. The lobe (Fig. 191) is constricted in front of the eyes. Chelicerae: the lateral striae of the female are more widely spaced than in *W. weber*; those of the male are moderately closely spaced. Abdomen: black. Sternum: orange, with blackish margins. Legs: orange. TmI: female 0.40-0.42, male 0.43-0.45. Male palp: Fig. 199. Epigynum: Fig. 209.

Diagnosis.—The male of *W. occidentalis* is diagnosed by the palpal tibia (Fig. 199); this is similar to that of *W. reclusa* (Fig. 200), but the angle between the principal and lateral apophyses is wider in *W. occidentalis*. The carapace lobe in *W. occidentalis* is more constricted than in *W. reclusa* (Fig. 191 cf. Fig. 192). The female of *W. occidentalis*



Figs. 194-202.—Male palpal tibiae, dorsal. 194, *W. tricornis*; 195, *W. palustris*; 196, *W. bifida*; 197, *W. serrata*; 198, *W. helenae*; 199, *W. occidentalis*; 200, *W. reclusa*; 201, *W. septentrionalis*; 202, *W. columbia* (Scale lines 0.1 mm).

can only be diagnosed by the epigynum (Fig. 209), but it is questionable whether this can be distinguished from those of *W. weber*, *W. helenae*, *W. reclusa*, *W. septentrionalis* and *W. columbia*.

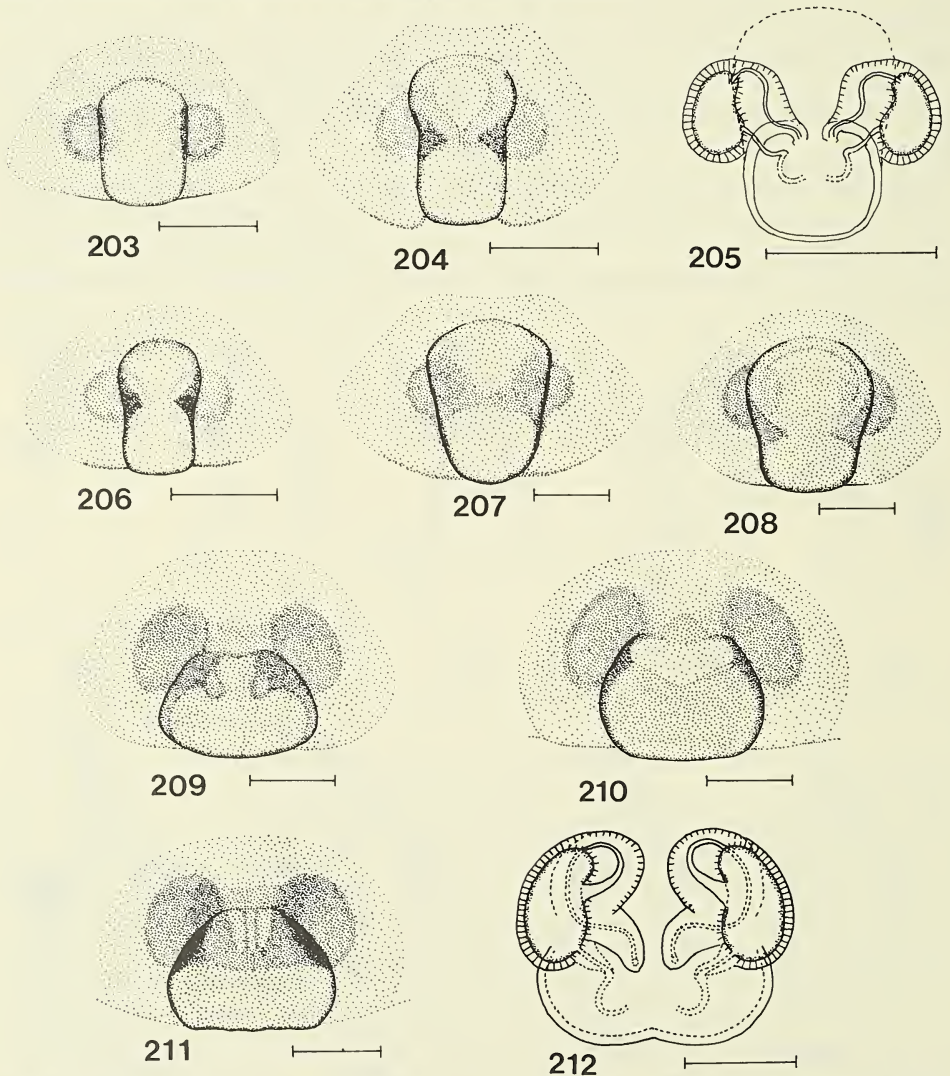
Distribution.—Known only from the type locality (Map 18).

Natural History.—Both sexes were adult in March; nothing was recorded on habitat.

Walckenaeria helenae, new species

Figs. 198, 211; Map 16

Type.—Male holotype from Last Chance Gulch, Helena, Lewis and Clark Co., Montana, 3 October 1964 (J. and W. Ivie); deposited in AMNH.



Figs. 203-212.—Epigyna, ventral. 203, *W. palustris*; 204, *W. aprilis*; 205, *W. palustris*, internal genitalia, cleared; 206, *W. palustris*, Manitoba specimen; 207, *W. solivaga*; 208, *W. anceps*; 209, *W. occidentalis*; 210, *W. weber*; 211, *W. helenae*; 212, *W. columbia*, internal genitalia, cleared (Scale lines 0.1 mm).

Description.—The male and female were taken together. Total length: female 2.2-2.3 mm, male 2.0 mm. Carapace: length: female 0.9-1.0 mm, male 0.9 mm. Orange-brown with dusky markings in the female, dark brown in the male. The male lobe is broad and scarcely constricted (as in *W. reclusa*: Fig. 192). Chelicerae: the lateral striae of the female are rather less widely spaced than in *W. weber*; in the male they are moderately spaced. Abdomen: grey to black. Sternum: orange, suffused with black on margins. Legs: orange. TmI: female 0.40-0.47, male 0.41-0.45. Male palp: Fig. 198. Epigynum: Fig. 211.

Diagnosis.—The male of *W. helenae* is diagnosed by the palpal tibia (Fig. 198); this is of the same pattern as those of *W. occidentalis* and *W. reclusa*, but significantly shorter (Fig. 198, cf. Figs. 199, 200). The female epigynum (Fig. 211) is probably indistinguishable from those of *W. weber*, *W. reclusa*, *W. occidentalis*, *W. septentrionalis* and *W. columbia*, and the female cannot therefore be safely diagnosed unless it is taken with a male.

Distribution.—Known only from the type locality (Map 16). This species was taken at the same time and place as *W. solivaga*.

Natural History.—Both sexes were adult in October; nothing was recorded on habitat.

Walckenaeria reclusa, new species

Figs. 187, 192, 200; Map 17

Type.—Male holotype from N.E. of McCall, Valley Co., Idaho, 31 May 1944 (W. Ivie); deposited in AMNH.

Description.—The female described was taken very close to the type locality, but not with a male. Total length: female 2.1 mm, male 1.9-2.0 mm. Carapace: length: female 0.90 mm, male 0.80-0.85 mm. Deep orange. The male lobe is broad and not much constricted (Fig. 192). Chelicerae: the lateral striae are fairly widely spaced in the female, moderately spaced in the male. Abdomen: black. Sternum: orange, with a black margin. Legs: orange. TmI: female/male 0.40-0.45. Male palp: Fig. 200.

Diagnosis.—*W. reclusa* male is diagnosed by the palpal tibia (Fig. 200); the lateral apophysis is very similar to that of *W. occidentalis* (Fig. 199), and for the distinguishing characters, see *W. occidentalis* diagnosis. The female epigynum seems to be indistinguishable from those of *W. weber*, *W. occidentalis*, *W. helenae*, *W. septentrionalis* and *W. columbia*, and the female cannot be diagnosed unless taken with the male.

Distribution.—Known only from the type locality (Map 17).

Natural History.—The female was adult in October, the male in May, August and October; nothing was recorded on habitat.

Walckenaeria septentrionalis, new species

Fig. 201; Map 18

Type.—Male holotype from Sidney, Vancouver Island, British Columbia, 16 September 1935 (Chamberlin and Ivie); deposited in AMNH.

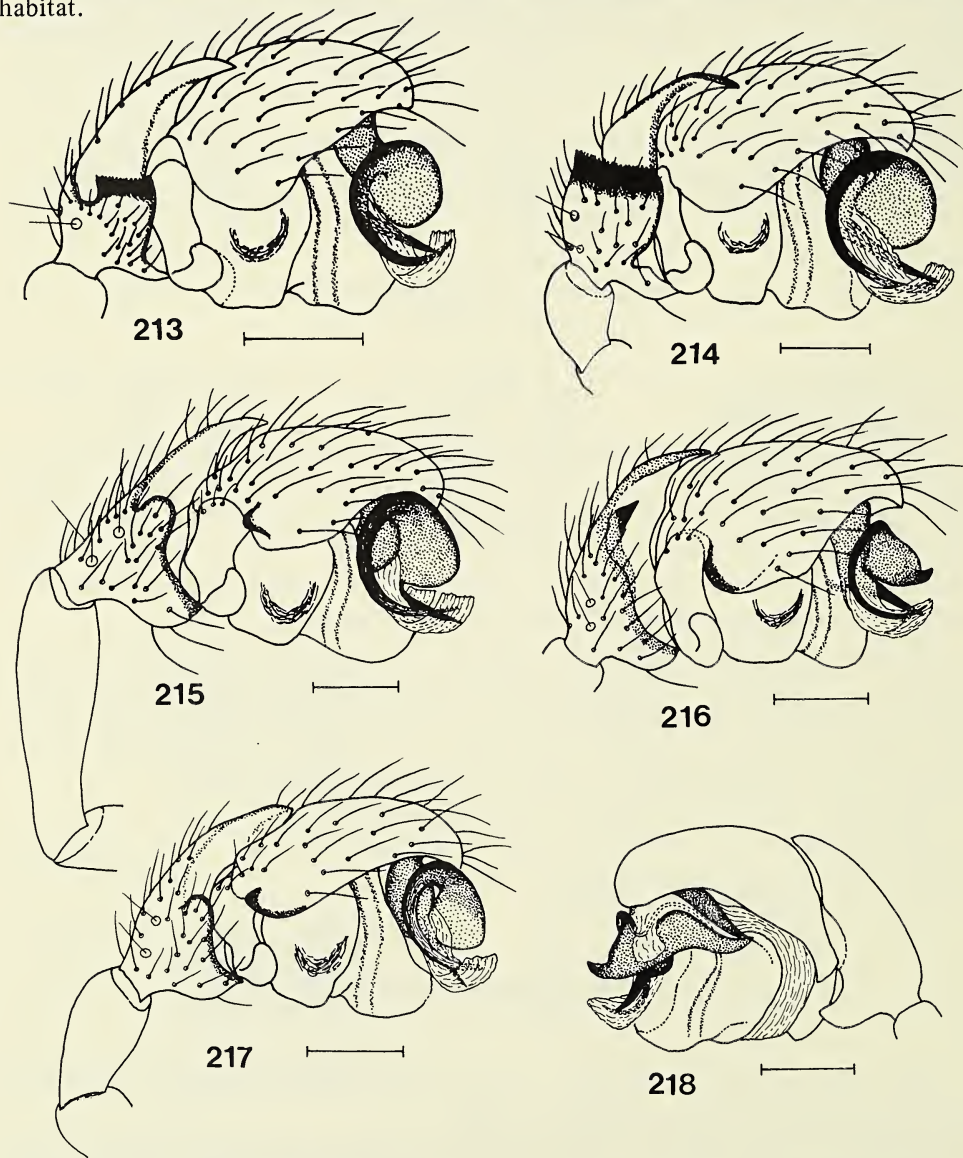
Description.—The male and female were taken together. Total length: female 2.5 mm, male 2.45 mm. Carapace: length: female/male 1.0 mm. Orange, with dusky markings. The male lobe is broad, as in *W. reclusa* (Fig. 192). Chelicerae: the lateral striae are moderately spaced in the female, fairly closely spaced in the male. Abdomen: grey to black.

Sternum: orange, with margins blackish. Legs: orange. TmI: female 0.45-0.47, male 0.40-0.42. Male palp: Fig. 201.

Diagnosis.—*W. septentrionalis* male is diagnosed by the palpal tibia (Fig. 201); the lateral apophysis is of the same form as that present in *W. occidentalis* and *W. reclusa*, but this apophysis, and the whole palp, are significantly larger ((Fig. 201 cf. Figs. 199, 200). The female epigynum seems to be indistinguishable from those of *W. weber*, *W. occidentalis*, *W. helenae*, *W. reclusa* and *W. columbia*, and the female cannot be diagnosed unless taken with the male.

Distribution.—Known only from the type locality (Map 18).

Natural History.—Both sexes were adult in September; nothing was recorded on habitat.



Figs. 213-218.—Male palps. 213, *W. exigua*, ectal; 214, *W. thrinax*, ectal; 215, *W. emarginata*, ectal; 216, *W. pinocchio*, ectal; 217, *W. monoceras*, ectal; 218, *W. pinocchio*, mesal (Scale lines 0.1 mm).

Walckenaeria columbia, new species

Fig. 202, 212; Map 18

Type.—Male holotype from Manning Provincial Park, British Columbia, 20 June-3 July 1979 (C. D. Dondale); deposited in CNC.

Description.—The male and female were taken together. Total length: female 2.65-2.90 mm, male 2.1 mm. Carapace: length: female 0.95-1.0 mm, male 0.90 mm. Orange-brown to dark brown, with dusky markings. The male lobe is broad as in *W. reclusa* (Fig. 192). Chelicerae: the lateral striae are moderately spaced in both sexes. Abdomen: grey to black. Sternum: orange, with dusky markings and margins. Legs: yellow to orange. TmI: female 0.45-0.47, male 0.40-0.50. Male palp: Fig. 202. Epigynum: Fig. 212.

Diagnosis.—*W. columbia* male is diagnosed by the palpal tibia (Fig. 202); the lateral apophysis is similar to that of *W. septentrionalis*, but is shorter and broader and less projecting (Fig. 202 cf. Fig. 201). The female epigynum is indistinguishable from those of *W. weber*, *W. occidentalis*, *W. helenae*, *W. reclusa* and *W. septentrionalis*, and the female cannot be diagnosed unless taken with the male.

Distribution.—Known only from the type locality (Map 18).

Natural History.—Both sexes were taken in June-July, in a pitfall in a rhododendron flat.

minuta Group

The males of this group have very similar palpal organs, and diagnosis is based on the form of the carapace horn, sometimes coupled with the form of the palpal tibia. The females fall into two groups on the basis of two distinct forms of epigynum; within these groups, the epigyna differ sufficiently from one another to make diagnosis relatively easy.

Partial keys to species

Males

1. Ocular area with small protuberance (Fig. 232) *cornuella*
 Ocular area with a distinct horn 2
2. Horn short and semi-vertical (Figs. 229, 230, 231)
 *minuta*, *exigua*, *thrinax* (see species descriptions)
 Horn longer and directed forwards
 *monoceras*, *pinocchio*, *emarginata* (see species descriptions)

Females

1. Epigyna as Figs. 242, 243, 244, 245
 *minuta*, *exigua*, *tenella*, *thrinax* (see species descriptions)
 Epigyna as Figs. 246, 247, 248, 249
 *cornuella*, *monoceras*, *placida*, *emarginata* (see species descriptions)

Walckenaeria minuta (Emerton)

Figs. 219, 221, 229, 233, 242, 250; Map 19

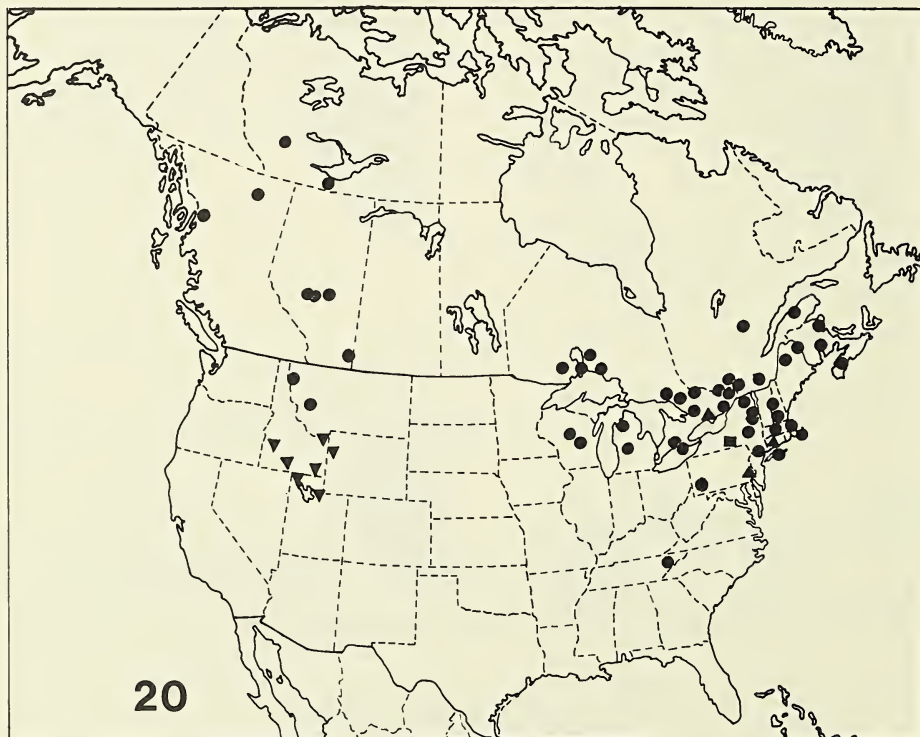
Cornicularia minuta Emerton 1882:42; Crosby and Bishop 1931:371; Roewer 1942:663; Kaston 1948:168; Bonnet 1956:1225.

Walckenaeria (*Microcornicularia*) *minuta*: Wunderlich 1972:388.

Type.—Male holotype from Mt. Carmel, Hamden, New Haven Co., Connecticut, 9 October 1881; in Emerton Collection, MCZ, examined.

Description.—Total length: female 1.45-1.60 mm, male 1.4-1.5 mm. Carapace: length: female/male 0.65 mm. Orange to pale brown. The male has a small horn, which is slightly bifid distally (Figs. 229, 233). Chelicerae: the lateral striae are moderately spaced in both sexes. Abdomen: grey to whitish grey. Sternum: yellow, with dusky margins. Legs: orange to orange-brown. TmI: female/male 0.35-0.40. Male palp: Figs. 219, 221. Epigynum: Figs. 242, 250.

Diagnosis.—The male of *W. minuta* is diagnosed by the small horn on the carapace (Figs. 229, 233), coupled with the form of the palpal tibia. Viewed dorsally, the lateral tibial apophysis is narrower in *W. minuta* (Fig. 221) than in the closely related species *W. exigua* (Fig. 222-224) and *W. thrinax* (Fig. 225); viewed laterally, it is narrower, and the fringe of coarse black hairs is more inclined, than in either *W. exigua* or *W. thrinax* (Fig. 219 cf. Figs. 220, 214). The hollow between the lateral and the principal apophyses is wide in *W. minuta*, and decreases in width through *W. exigua* to *W. thrinax*. The carapace horns in *W. minuta* and *W. exigua* are virtually identical, but in *W. thrinax* the horn is somewhat broader (Figs. 231, 234, cf. Figs. 229, 233). The female of *W. minuta* is diagnosed by the epigynum (Fig. 242); the spermathecae and associated structures are seen through the integument to be more upright and less broad than in *W. exigua* (Fig. 243); there is a clear difference in the internal genitalia of these two species (Fig. 250 cf. Fig. 251). *W. minuta* is readily distinguished from *W. tenella* by the epigynum (Fig. 242 cf. Fig. 245), by the wider spacing of the cheliceral striae in *W. minuta*, and by the



Map 20.—North America. Distributions of *W. exigua* (circles), *W. pinocchio* (triangles), *W. thrinax* (inverted triangles) and *W. placida* (square).

stouter legs of *W. tenella* (MT I 1/d and tarsus I 1/d are 3.5-4 in *W. tennella*, 5 in *W. minuta*). *W. minuta* female is distinguished from *W. thrinax* by the epigynum (Fig. 242 cf. Fig. 244), by the significantly larger size of *W. thrinax* and probably also by the geographical distributions.

Distribution.—This species has been taken in the eastern and central parts of the U.S.A. (Map 19); the record shown for New Mexico is based on a female which shows small differences from the eastern populations and may prove to be another species. There are no records for Canada.

Natural History.—Adult females have been taken in April, May October and November, males in January, March-May and September-November. Nothing was recorded on habitat.

Walckenaeria exigua, new species

Figs. 213, 220, 222, 223, 224, 230, 243, 251; Map 20)

Type.—Male holotype from Island 1024, Lake Temagami, Ontario, 15-25 August 1946 (Gertsch, Ivie and Kurata); deposited in AMNH.

Description.—The two sexes have been taken together on many occasions. Total length: female 1.55-1.75 mm, male 1.35-1.75 mm. Carapace: length: female 0.65-0.75 mm, male 0.65-0.70 mm. Orange-brown to chestnut brown, often slightly darkened anteriorly. The male has a small horn (Fig. 230), similar to that of *W. minuta*. Chelicerae: the lateral striae are moderately spaced in the female, more closely spaced in the male, Abdomen: grey to black. Sternum: orange to brown, with margins suffused with black. Legs: yellow to orange-brown. TmI: female 0.40-0.45, male 0.36-0.42. Male palp: Figs. 213, 220, 222, 223, 224. Epigynum: Figs. 243, 251; there are small variations in the position and shape of the spermathecae.

Diagnosis.—This species has been confused in the past, even by Emerton himself, with *W. minuta*, and many of the specimens labelled "*W. minuta*" in the museum collections are *W. exigua*. The separation of *W. exigua* male from *W. minuta* is dealt with under *W. minuta* diagnosis. *W. exigua* male is distinguished from *W. thrinax* by the form of the palpal tibia, the lateral apophysis being narrower, and the hollow between the lateral and the principal apophyses wider, in *W. exigua* than in *W. thrinax* (Figs. 222-224 cf. Fig. 225); *W. thrinax* is also significantly larger in size. *W. exigua* female is diagnosed by the epigynum (Fig. 243); there is no problem in distinguishing the epigyna of *W. minuta* (Fig. 242; see *W. minuta* diagnosis) or of *W. tenella* (Fig. 245). The epigynum of *W. thrinax* (Fig. 244) is quite similar to that of *W. exigua*, but distinguishable, if only by its size: the width of the posterior plate in *W. exigua* is 0.110-0.125 mm, in *W. thrinax* 0.155-0.165 mm. *W. thrinax* is also significantly larger in size than *W. exigua*, and the leg proportions are different: e.g., MTI/tI is 1.25-1.3 for *W. thrinax* female, and 1.1 for *W. exigua* female.

Distribution.—*W. exigua* is distributed widely over the northern part of the continent (Map 20).

Natural History.—Adult females have been taken in all months except January, March and December, males in all months except March, November and December. Habitats recorded are in sphagnum, on dunes, in fields or grass, in leaf litter and in woods.

Walckenaeria tenella, new species

Fig. 245; Map 19

Type.—Female holotype from Janis Point, Ulster Co., New York, 24 May 1920 (S. C. Bishop); deposited in AMNH.

Description.—Only the female is known. Total length: female 1.60 mm. Carapace: length: female 0.62 mm. Orange, with faint dusky markings. Chelicerae: lateral striae closely spaced. Abdomen: grey-black. Sternum: orange-yellow. Legs: orange-yellow; short and stout, with MTI 1/d and tarsus I 1/d 3.5-4. TmI: female 0.41-0.45. Epigynum: Fig. 245.

Diagnosis.—*W. tenella* female is diagnosed by the epigynum (Fig. 245), the closely spaced cheliceral striae, and the stout legs (see *W. minuta* diagnosis).

Distribution.—Known only from two localities in the northeast (Map 19).

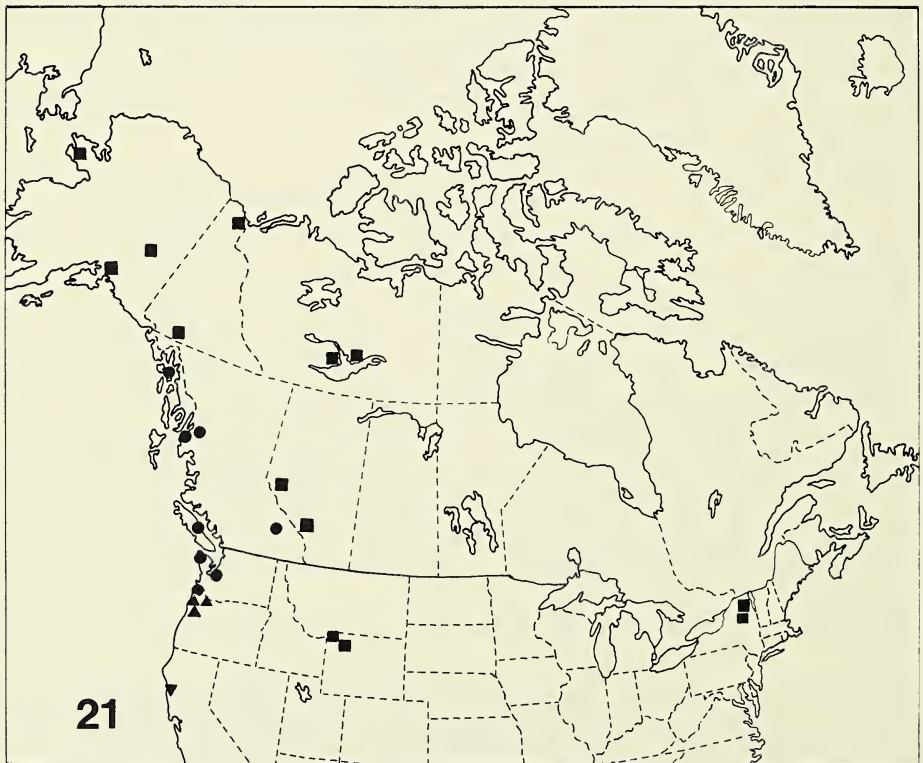
Natural History.—Adult females have been taken in May and August; nothing was recorded on habitat.

Walckenaeria thrinax (Chamberlin and Ivie)

Figs. 214, 225, 231, 234, 244; Map 20

Cornicularia thrinax Chamberlin and Ivie 1933:24; Roewer 1942:664; Bonnet 1956:1225.

Walckenaeria (Pseudocornicularia) thrinax: Wunderlich 1972:388.

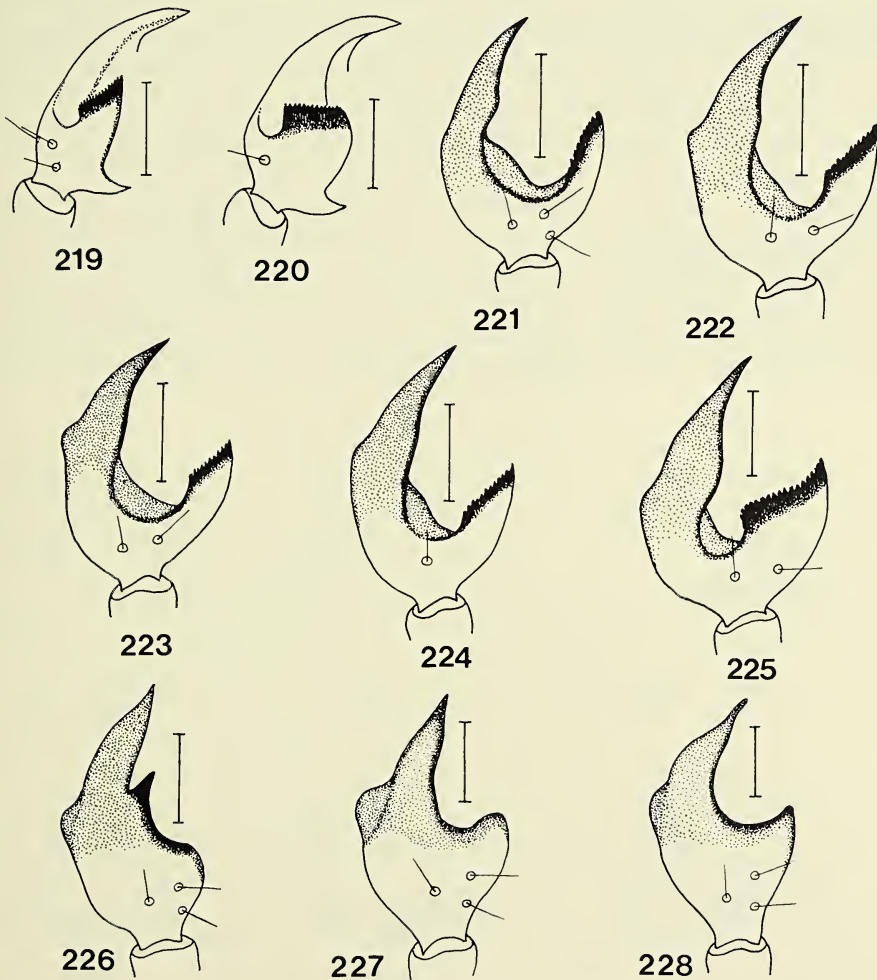


Map 21.—North America. Distributions of *W. cornuella* (circles), *W. monoceras* (triangles), *W. emarginata* (inverted triangle) and *W. holmi* (squares).

Type.—Male holotype from Dove Creek, Raft River Mtns., Boxelder Co., Utah, 9 September 1936 (Chamberlin and Ivie); in AMNH, examined.

Description.—Total length: female 1.9-2.1 mm, male 1.9-2.0 mm. Carapace: length: female 0.80-0.90 mm, male 0.80-0.85 mm. Orange to orange brown, with dusky markings. The male has a short, broad horn (Figs. 231, 234). Chelicerae: the lateral striae are moderately spaced in both sexes. Abdomen: grey to black. Sternum: orange, with blackish margins. Legs: orange-yellow. TmI: female/male 0.40-0.42. Male palp: Figs. 214, 225. Epigynum Figs. 244; the shape of the spermathecae and of the posterior area show some variations.

Diagnosis.—*W. thrinax* male is diagnosed by the male carapace horn (Figs. 231, 234) and by the form of the palpal tibia (Figs. 214, 225); see *W. minuta* diagnosis. *W. thrinax* female is diagnosed by the epigynum (Fig. 244), which though rather similar to that of *W. exigua* (Fig. 243) is distinguishable (see *W. exigua* diagnosis).



Figs. 219-228.—Male palpal tibiae. 219, *W. minuta*, ectal; 220, *W. exigua*, ectal; 221, *W. minuta*, dorsal; 222, *W. exigua*, type, dorsal; 223, *W. exigua*, New Brunswick specimen, dorsal; 224, *W. exigua*, British Columbia specimen, dorsal; 225, *W. thrinax*, dorsal; 226, *W. pinocchio*, dorsal; 227, *W. cornuella*, dorsal; 228, *W. emarginata*, dorsal (Scale lines 0.1 mm).

Distribution.—Recorded only from a limited area in Utah, Wyoming and Idaho (Map 20).

Natural History.—Adult females have been taken in June-September, males in August. Nothing was recorded on habitat.

Walckenaeria cornuella (Chamberlin and Ivie), new combination

Figs. 227, 232, 246; Map 21

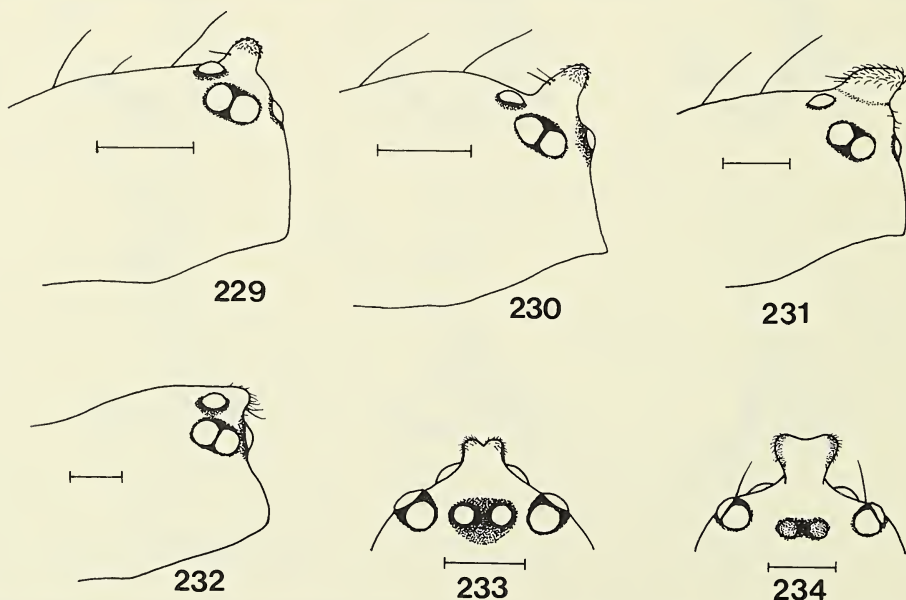
Sisicottus cornuella Chamberlin and Ivie 1939:65; Bonnet 1958:4065.

Sisicottus cornuellus: Roewer 1942:650.

Type.—Male holotype from Jack Horner Creek, near Nehalem, Tillamook Co., Oregon, 25 August 1936 (W. Ivie); in AMNH, examined.

Description.—Total length: female 2.45 mm, male 2.1-2.2 mm. Carapace: length: female 1.10 mm, male 0.95-1.05 mm. Orange to deep orange, with faint dusky markings. The male has a small projection or "horn" in the ocular area (Fig. 232). Chelicerae: the lateral striae are moderately spaced in both sexes. Abdomen: grey-black. Sternum: orange, with dusky margins. Legs: yellow to orange. TmI: female 0.40, male 0.35-0.38. Male palp: Fig. 227; the palpal organs, apart from being somewhat larger in size, are indistinguishable from those of *W. monoceras* (Fig. 217). Epigynum: Fig. 246.

Diagnosis.—*W. cornuella* is diagnosed by the small projection arising from the ocular area (Fig. 232), and confirmed by the form of the palpal tibia (Fig. 227). The female is diagnosed by the epigynum (Fig. 246), which seems to be distinguishable from that of *W. monoceras* (Fig. 248) by the somewhat shorter convergent lines enclosing the posterior area and by the less elongated spermathecae. *W. cornuella* female is normally larger in size than *W. monoceras*, and the legs are marginally slimmer (tibia I 1/d 5 for *W. cornuella*, 4



Figs. 229-234.—Male carapaces. 229. *W. minuta*, lateral; 230, *W. exigua*, lateral; 231, *W. thrinax*, lateral; 232, *W. cornuella*, lateral; 233, *W. minuta*, in front; 234, *W. thrinax*, in front (Scale lines 0.1 mm).

for *W. monoceras*). The epigyna of *W. cornuella* and *W. emarginata* (Fig. 249) seem to be distinguishable, and the anterior elevation of the carapace in *W. emarginata* will confirm the separation.

Distribution.—Recorded only from the northwestern coastal area of N. America (Map 21).

Natural History.—Adult females have been taken in June-September, males in May-July. The only habitat recorded was in woods.

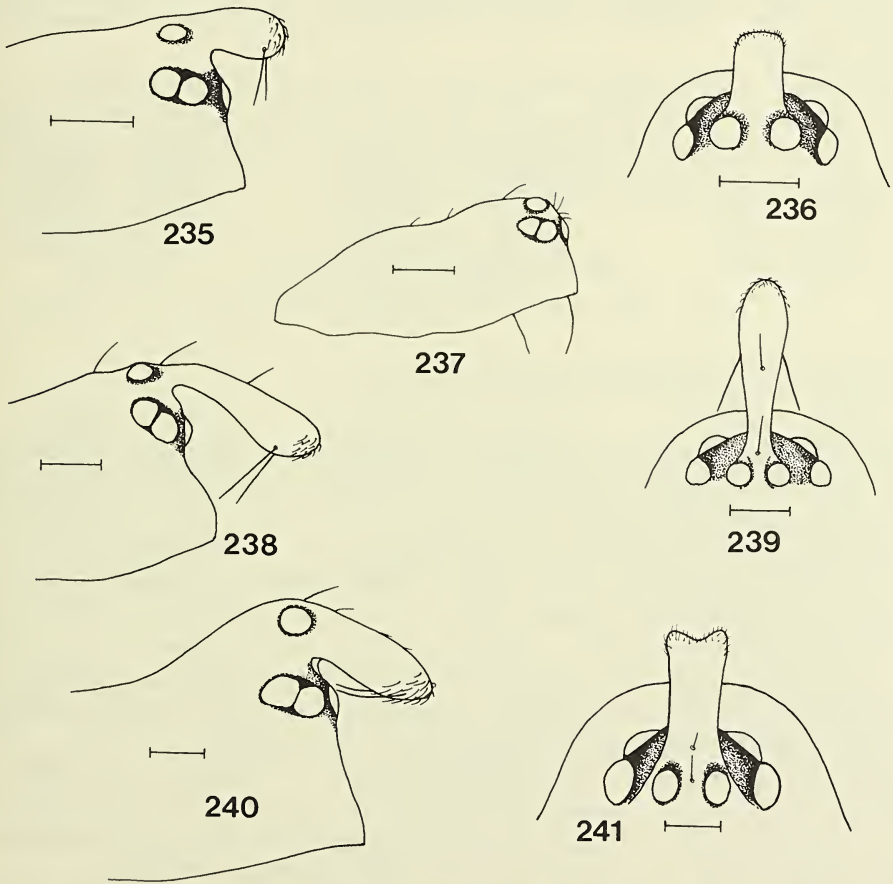
Walckenaeria monoceras (Chamberlin and Ivie)

Figs. 217, 235, 236, 248, 252; Map 21

Cornicularia monoceras Chamberlin and Ivie 1947:33.

Walckenaeria (Kastonia) monoceras: Wunderlich 1972:389.

This species should not be confused with the European species *W. (Prosopotheca) monoceros* (Wider).



Figs. 235-241.—Carapaces. 235, *W. monoceras*, male, lateral; 236, *W. monoceras*, male, dorsal; 237, *W. emarginata*, female, lateral; 238, *W. pinocchio*, male lateral; 239, *W. pinocchio*, male, dorsal; 240, *W. emarginata*, male, lateral; 241, *W. emarginata*, male dorsal (Scale lines 0.1 mm).

Type.—No types seem to have been designated. One vial of *Cornicularia monoceras* (2 males, one female) in AMNH has a pencilled label of the locality which agrees with the type locality given by Chamberlin and Ivie (1947), namely, N. of Monroe, Benton Co., Oregon, 3 March 1937 (J. C. Chamberlin). One male has been selected from this vial and labelled "Lectotype"; this is deposited in AMNH.

Description.—Total length: female 2.0-2.2 mm, male 1.85-2.0 mm. Carapace: length: female/male 0.82-0.90 mm. Orange to orange-brown, with dusky markings. The male has a rather bulbous horn arising from the ocular area (Figs. 235, 236); the distal end of the horn bears short hairs, and two long bristles project downwards from near the distal end. Chelicerae: the lateral striae are fairly closely spaced in both sexes. Abdomen: grey to black. Sternum: orange, with dusky margins. Legs: orange. TmI: female 0.37, male 0.35. Male palp: Fig. 217. Epigynum: Figs. 248, 252.

Diagnosis.—The male of *W. monoceras* is diagnosed by the form of the horn (Figs. 235, 236), which distinguishes this species from all others; confirmation is given by the form of the male palp (Fig. 217). The carapace horns of *W. pinocchio* and *W. emarginata* are generally similar, but longer. *W. monoceras* female is diagnosed by the epigynum (Fig. 248), which is probably distinguishable from those of *W. cornuella* (see *W. cornuella* diagnosis) and *W. emarginata* (Fig. 249); the anterior elevation of the carapace in *W. emarginata* (Fig. 237), which is absent in *W. monoceras*, will confirm the separation of these two species.

Distribution.—Known only from the western coastal area of Oregon (Map 21).

Natural History.—Adult females have been taken in March, November and December, males in February, March, April, November and December. Habitats recorded are in moss near a stream, and in douglas fir litter.

Walckenaeria pinocchio (Kaston)
Figs. 216, 218, 226, 238, 239; Map 20

Cornicularia pinocchio Kaston 1945:7; and 1948:168.

Walckenaeria (Kastonia) pinocchio: Wunderlich 1972:389.

Type.—Male holotype from Mt. Carmel, New Haven Co., Connecticut, 19 April 1935 (B. J. Kaston); in AMNH, examined. This type is in bad condition, with one palp, all the legs and the carapace horn missing.

Description.—Only the male is known (but see *W. placida*). Total length: male 1.8-2.0 mm (excl. horn). Carapace: length: male 0.70-0.90 (excl. horn). Brown, with dusky markings. There is a long horn projecting from the ocular area (Figs. 238-239); the distal end of this horn bears short hairs, and two long bristles project towards the clypeus from near the distal end. Chelicerae: the lateral striae are fairly closely spaced. Abdomen: grey. Sternum: orange, with dusky markings. Legs: yellow-brown. TmI: male 0.40. Male palp: Figs. 216, 218, 226; the anterior end of the ED has a sharp point.

Diagnosis.—*W. pinocchio* male is diagnosed by the very distinctive horn (Figs. 238, 239), and diagnosis is confirmed by the form of the palpal tibia (Fig. 226) and by the pointed anterior end of the ED (fig. 218). *W. emarginata* has the carapace horn of rather similar length, but this horn is stouter and bifid at the tip (Figs. 240, 241).

Distribution.—The only three records are from the northeastern part of the continent (Map 20).

Natural History.—Adult males were taken in May and October; nothing was recorded on habitat.

Walckenaeria placida (Banks)

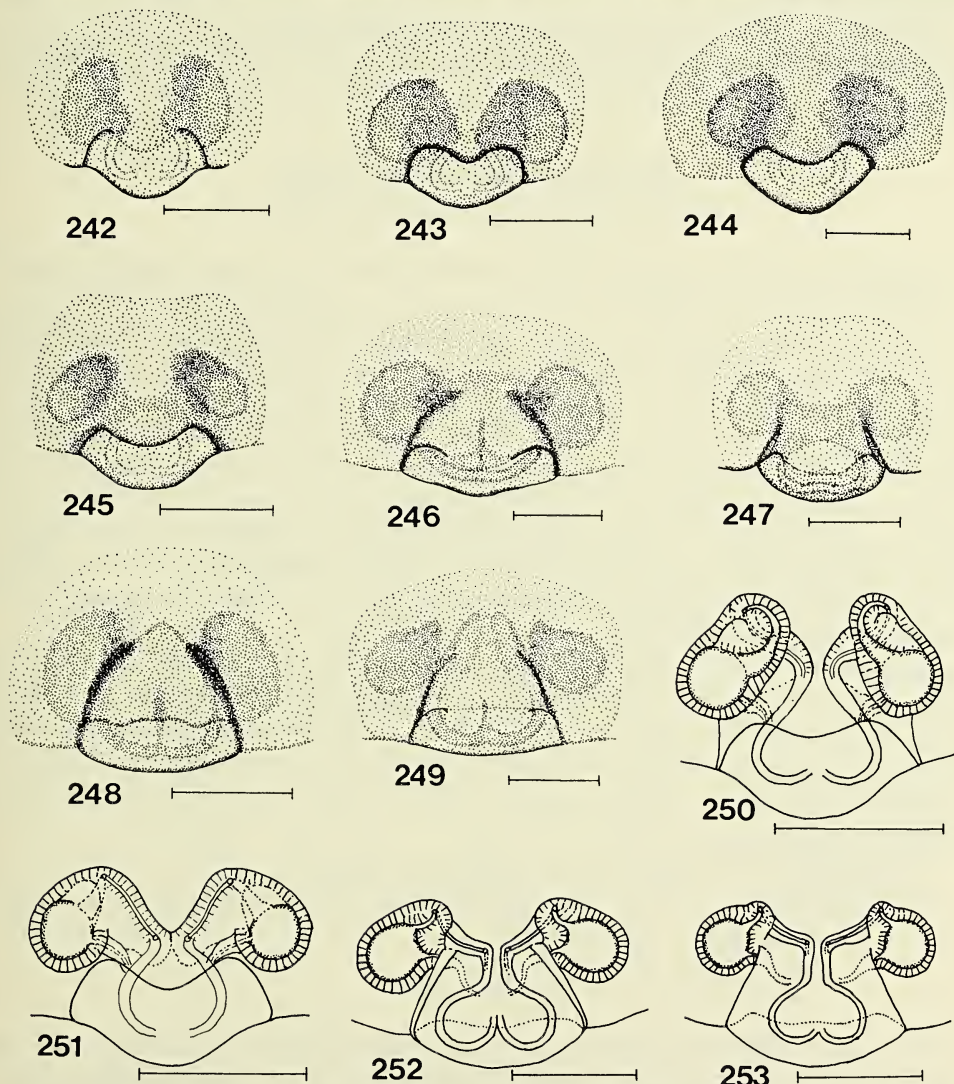
Figs. 247, 253; Map 20

Cornicularia placida Banks 1892:35, and 1916:72; Crosby and Bishop 1931:373; Roewer 1942:664; Bonnet 1956:1225.

Walckenaeria (*Cornicularia*) *placida*: Wunderlich 1972:385.

Type.—Female holotype from Fall Creek, Ithaca, Tompkins Co., New York; in MCZ, examined. This type is very faded in color, and most of the legs are missing.

Description.—Only the female is known. Total length: female 2.0 mm. Carapace: length: female 0.90 mm. Orange. Chelicerae: lateral striae fairly widely separated. Abdomen: whitish grey. Sternum: yellow, darker on margins. Legs: pale yellow. Epigynum:



Figs. 242-253.—Epigyna, ventral. 242, *W. minuta*; 243, *W. exigua*; 244, *W. thrinax*; 245, *W. tenella*; 246, *W. cornuella*; 247, *W. placida*; 248, *W. monoceras*; 249, *W. emarginata*; 250, *W. minuta*, internal genitalia, cleared; 251, *W. exigua*, internal genitalia, cleared; 252, *W. monoceras*, internal genitalia, cleared; 253, *W. placida*, internal genitalia, cleared (Scale lines 0.1 mm).

Figs. 247, 253; in fresh specimens the integument of the epigynum would be more deeply pigmented and less transparent. It is possible that *W. placida* is the female of *W. pinocchio* (the name *placida* would have priority). The epigynum (external and internal) is of the form to be expected, being generally similar to those of *W. cornuella* and *W. monoceras*, and the localities of capture of *W. placida* and *W. pinocchio* are in the same geographical area (Map 18). This matter cannot be resolved until both sexes of *W. pinocchio* are taken together, and the female compared with *W. placida*.

Diagnosis.—The female of *W. placida* must be diagnosed by the epigynum (Figs. 247, 253); the unique specimen is however rather bleached, and fresh specimens would no doubt have a somewhat different appearance, being perhaps more similar to *W. cornuella* (Fig. 246). Until further specimens become available, the diagnosis must remain somewhat uncertain.

Distribution.—Known only from the type locality (Map 20).

Natural History.—The type female was taken in October; nothing was recorded on habitat.

Walckenaeria emarginata, new species

Figs. 215, 228, 237, 240, 241, 249; Map 21

Type.—Male holotype from Mendocino, Mendocino Co., California, 1 January 1958 (J. R. Helfer); deposited in AMNH.

Description.—The female described came from the type locality, but on a different date. Total length: female 2.3 mm, male 2.25 mm (excl. horn). Carapace: length: female 1.1 mm, male 1.0 mm (excl. horn). Orange-brown. The female carapace is raised anteriorly (Fig. 237). The male horn is stout, slightly notched distally, and slopes downwards (Figs. 240, 241); distally it bears short hairs, and from near the distal end two long bristles project backwards to the anterior median eyes. Chelicerae: the lateral striae are fairly closely spaced in the female, more widely separated in the male. Abdomen: grey to black. Sternum: orange. Legs: orange. TmI: female 0.45, male 0.40-0.45. Male palp: Fig. 215; the patella is long, and the tibia and palpal organs are of the same form as in *W. monoceras*. Epigynum: Fig. 249.

Diagnosis.—The male of *W. emarginata* is diagnosed by the distinctive carapace horn (Figs. 240, 241), which is notched at the tip. The palp is very similar to that of *W. monoceras*, but the patella is longer (Fig. 215 cf. Fig. 217). The female can be diagnosed by the epigynum (Fig. 249), which differs slightly from those of *W. cornuella* (Fig. 246) and *W. monoceras* (Fig. 248), coupled with the carapace profile (Fig. 237) and possibly the geographical distribution.

Distribution.—Known only from the type locality (Map 21).

Natural History.—The male was adult in June; nothing was recorded on habitat.

unicornis Group

This group contains five species in N. America. The males are readily diagnosed by the form of the palpal tibiae; the females can be diagnosed by the epigynum, although it is not always easy to separate *W. clavicornis* and *W. holmi*.

Partial keys to species

Males

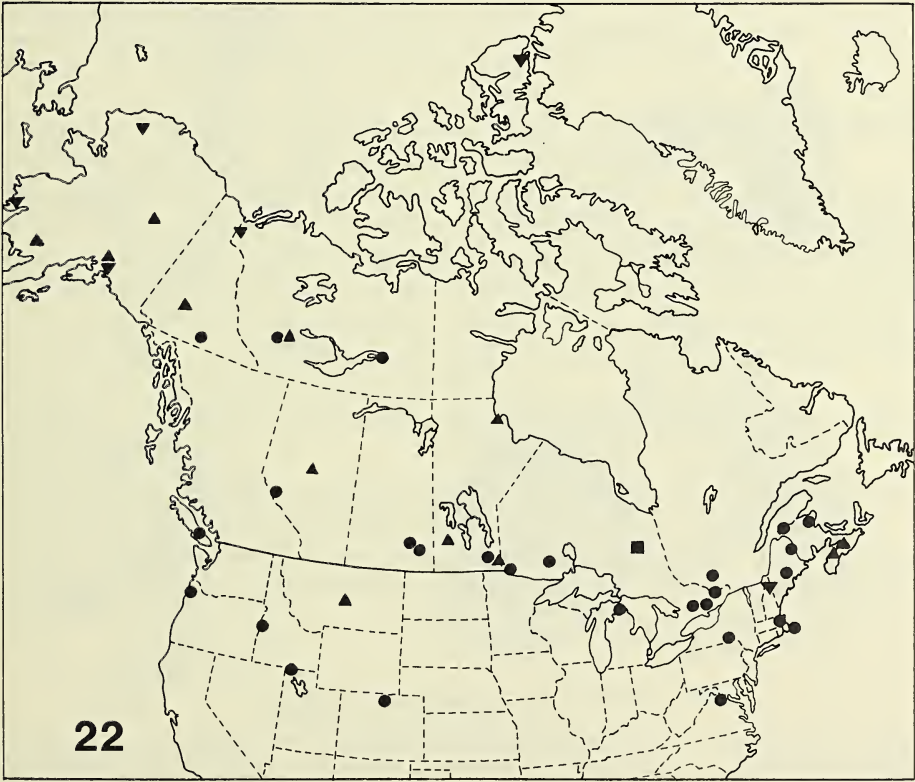
- 1. Palpal tibial apophyses intersecting (Figs. 262, 263)
 *clavicornis*, *holmi* (see species descriptions)
- Palpal tibial apophyses not intersecting
 *auranticeps*, *lepida* (see species descriptions)

Females

- 1. Epigynum with two tongue-like projections (Figs. 279-284)
 *clavicornis*, *holmi* (see species descriptions)
- Epigynum not of this form 2
- 2. Posterior area of epigynum enclosed by convex lines (Figs. 274, 276)
 *auranticeps*, *fusciceps* (see species descriptions)
- Posterior area of epigynum enclosed by concave lines (Fig. 275). *lepida*

Walckenaeria auranticeps (Emerton)
Figs. 254, 255, 257, 267, 268, 273, 276; Map 22

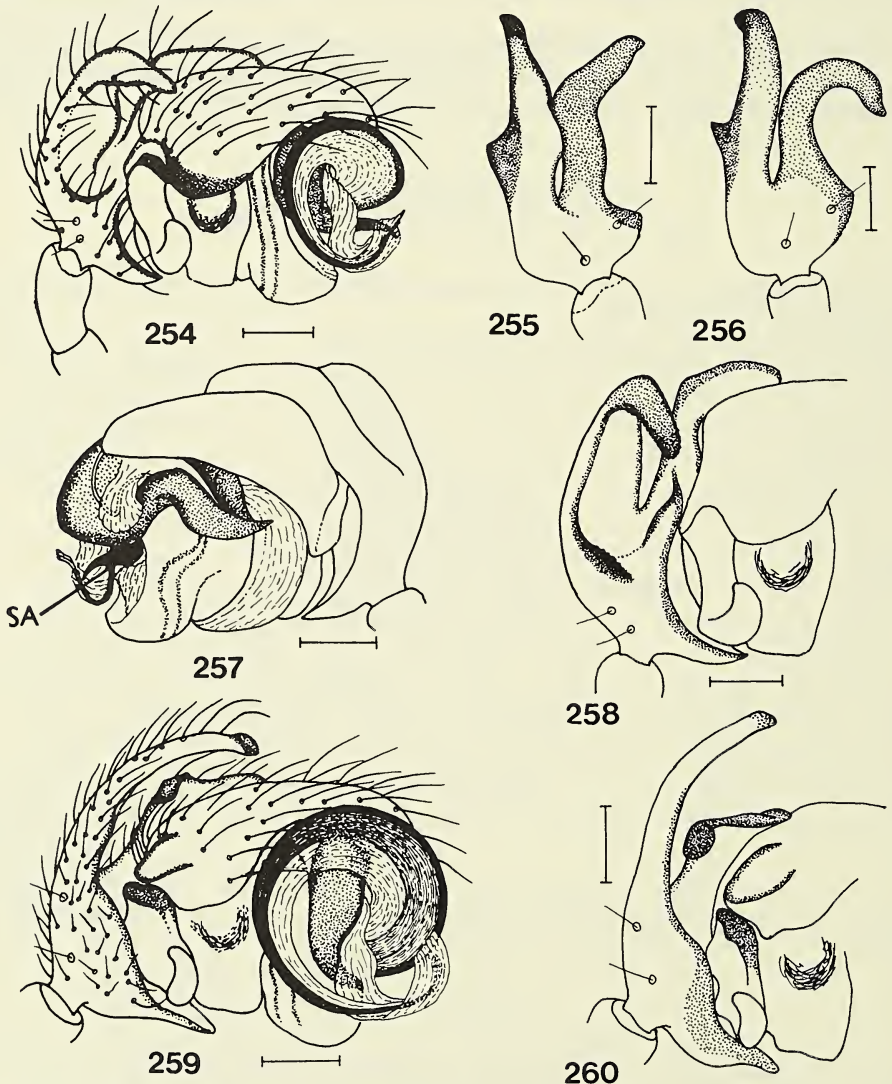
Cornicularia auranticeps Emerton 1882:43; Crosby and Bishop 1931:361; Roewer 1942:662; Kaston 1948:168; Bonnet 1956:1220.
Walckenaeria (*Cornicularia*) *auranticeps*: Wunderlich 1972:383.



Map 22.—North America. Distributions of *W. auranticeps* (circles), *W. lepida* (triangles), *W. clavicornis* (inverted triangles) and *W. fusciceps* (square).

Type.—Male and female syntypes from Clarendon Hills, Hyde Park, Suffolk Co., Massachusetts, 24 March 1975; in Emerton Collection, MCZ, examined.

Description.—Total length: female 2.25-3.20 mm, male 2.0-2.2 mm. Carapace: length: female 1.0-1.2 mm, male 0.9-1.0 mm. Bright orange. The male has a broad, upright horn in the ocular area (Figs. 267, 268). Chelicerae: the lateral striae are closely spaced in both sexes. Abdomen: black. Sternum: orange, with dusky margins; a few minute pits are present. Legs: femora orange, remaining segments dark blackish brown. TmI: female/male 0.50-0.55. Male palp: Figs. 254, 255, 257. Epigynum: Figs. 273, 276; the shape of the posterior area is variable, but the margins are always convex. *W. auranticeps* is close to the European species *W. unicornis* (O. P.-Cambridge), but the color is different and there are small differences in the genitalia.



Figs. 254-260.—254, *W. auranticeps*, male palp, ectal; 255, *W. auranticeps*, male palpal tibia, dorsal; 256, *W. lepidus*, male palpal tibia, dorsal; 257, *W. auranticeps*, male palp, mesal; 258, *W. lepidus*, male palpal tibia, ectal; 259, *W. clavicornis*, male palp, ectal; 260, *W. holmi*, male palpal tibia, ectal. Abbreviation: SA, suprategular apophysis (Scale lines 0.1 mm).

Diagnosis.—The male of *W. auranticeps* is diagnosed by the horn on the carapace (Fig. 267), coupled with the form of the palpal tibia and of the palp (Figs. 254, 255). The closely related species *W. lepida* is distinguished from *W. auranticeps* by the form of the palpal tibia, in which the lateral apophysis curves outwards and downwards (Figs. 256, 258). The female of *W. auranticeps* is diagnosed by the epigynum (Fig. 273). The epigynum of *W. fusciceps* is similar, but has the central area broader, and the spermathecae are near to the posterior margin (Fig. 276); *W. fusciceps* is also different in color. In *W. lepida*, which has a similar color to that of *W. auranticeps*, the central area of the epigynum has concave margins as opposed to the convex margins of *W. auranticeps* (Fig. 274 cf. Fig. 273).

Distribution.—*W. auranticeps* is widely distributed over the central and northern parts of the continent (Map 22). It has on occasions been taken in the same area as *W. lepida*.

Natural History.—Adult females have been taken in March and May–October, males in March, May, June and August–November. Habitats are under leaves, in grass, and on low vegetation (by sweeping or beating).

Walckenaeria lepida (Kulczynski)

Figs. 256, 258, 274; Map 22

Cornicularia lepida Kulczynski 1885:39; Roewer 1942:661.

Walckenaera lepida; Bonnet 1959:4813.

Walckenaeria (*Cornicularia*) *lepida*: Wunderlich 1972:385.

Cornicularia pacifica Emerton 1923:242; Roewer 1942:663; Bonnet 1956:1225. I have confirmed this synonymy (Ivie 1967:127) by examination of Emerton's male type (MCZ).

Type.—The male holotype (Kamchatka, Siberia) is presumably in the Kulczynski Collection in Warsaw, but I have been unable to obtain it for examination.

Description.—The female, which has been taken with the male, is described for the first time. Total length: female 2.55 mm, male 2.0–2.45 mm. Carapace: length: female 1.0 mm, male 0.95–1.0 mm. Bright orange. The male has a horn in the ocular area, similar to that of *W. auranticeps*. Chelicerae: the lateral striae are fairly widely spaced in the female, but closely spaced in the male. Abdomen: black. Sternum: orange, with dusky margins. Legs: the femora are orange, the remaining segments brown. TmI: female/male 0.50–0.55. Male palp: Figs. 256, 258. Epigynum: Fig. 274.

Diagnosis.—This species is very similar to *W. auranticeps*, and its diagnosis is dealt with under that species.

Distribution.—*W. lepida* is distributed across the northern part of the continent, most of the records being from Canada (Map 22). The type locality is in eastern Asia.

Natural History.—Adult females have been recorded in April–July and in September, males in May, June and August. It has been taken on low vegetation and at ground level in traps.

Walckenaeria fusciceps, new species

Fig. 275; Map 22

Type.—Female holotype from Gregoire Mills, Ontario, 22 June–11 July 1973 (Redner and Starr); deposited in CNC.

Description.—Only the female is known. Total length: female 3.3 mm. Carapace: length: female 1.40 mm. Deep chestnut brown. Chelicerae: the lateral striae are widely spaced. Abdomen: grey-black. Sternum: deep chestnut brown, with blackish margins; the surface has numerous minute pits. Legs: orange. TmI: female 0.70. Epigynum: Fig. 275.

Diagnosis.—*W. fusciceps* female is diagnosed by the epigynum (Fig. 275) and the color (see *W. auranticeps* diagnosis); confirmation is offered by the high value of TmI (0.70).

Distribution.—Known only from the type locality (Map 22).

Natural History.—The type female was taken adult in June-July, in a pitfall in tall grass.

Walckenaeria clavicornis (Emerton)

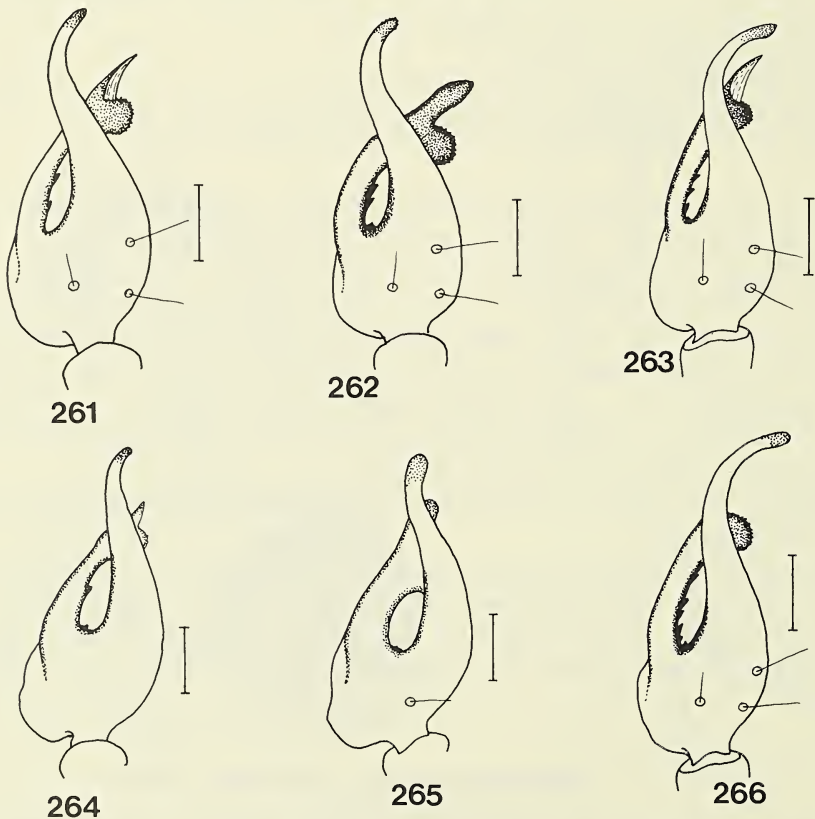
Figs. 5, 6, 259, 263, 266, 269, 270, 271, 272, 279, 281, 283; Map 22

Cornicularia clavicornis Emerton 1882:43; Holm 1967:24.

Cornicularia karpinskii: Braendegaard 1946:35; Locket and Millidge 1953:207 (misidentification) (*nec* *C. karpinskii* O.P.-Cambridge).

Walckenaeria (*Cornicularia*) *clavicornis*: Wunderlich 1972:383.

not Cornicularia clavicornis: Crosby and Bishop 1931: Figs. 18-23.

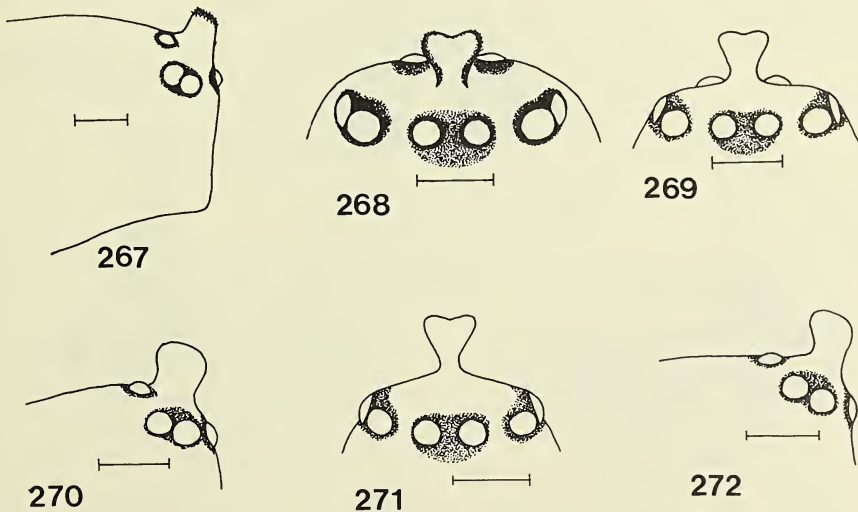


Figs. 261-266.—Male palpal tibiae. 261, *W. karpinskii*, type, dorsal; 262, *W. holmi*, dorsal; 263, *W. clavicornis*, dorsal; 264, *W. karpinskii*, type, meso-dorsal; 265, *W. holmi*, meso-dorsal; 266, *W. clavicornis*, another specimen, dorsal (Scale lines 0.1 mm).

Type.—Holotype male from Mt. Washington, Coos Co., New Hampshire, 11 June 1877; in MCZ, examined.

Description.—Total length: female 2.0-2.5 mm, male 2.0-2.3 mm. Carapace: length: female 0.9-1.0, male 0.90-0.95. Orange-brown to deep brown, with dusky markings. The male has a stout horn in the ocular area (Figs. 269-272) Chelicerae: the lateral striae are moderately spaced in both sexes. Abdomen: grey to black. Sternum: orange-brown, with dark margins. Legs: brown to orange-brown. TmI: female 0.50-0.54, male 0.47-0.50. Male palp: Figs. 259, 263, 266. Epigynum: Figs. 279, 281, 283; the entrances to the spermathecal ducts seem to lie beneath the plates (cf. Fig. 277).

Diagnosis.—The male is diagnosed by the form of the palp (Fig. 259) and the tibial apophyses (Figs. 263, 266). *W. clavicornis* is closely similar to *W. holmi*; the males are distinguished by the palpal tibiae. In *W. holmi* (Fig. 262) the mesal apophysis crosses the lateral apophysis to a greater extent than in *W. clavicornis*, and the distal end of the mesal apophysis is much stouter and blunter in *W. holmi* than in *W. clavicornis*. The female of *W. clavicornis* is diagnosed by the epigynum (Figs. 279, 281, 283), which has two tongue-like plates projecting posteriorly. *W. holmi* has a very similar epigynum, and in some cases it can be difficult to distinguish the females of these two species. Where the epigynal plates of *W. clavicornis* are "typical" in shape, with a distinct lateral bulge (Figs. 279, 281), separation from *W. holmi* (Figs. 278, 280, 282) is simple. Unfortunately, some females of *W. clavicornis* (taken with authentic males) have the plates very similar in shape to those of some specimens of *W. holmi* (Fig. 283 cf. Fig. 278); where this is the case, recourse must be made to the length of the plates, which in *W. clavicornis* are usually up to 0.15 mm, while in *W. holmi* they are ca. 0.18 mm and upwards (Holm 1967). Females of *W. holmi* seem always to have a plate length of at least 0.18 mm, but in some specimens of *W. clavicornis* the plate length exceeds 0.15 mm; in instances of this kind, the two species can probably be distinguished by the fact that in *W. holmi* the plates extend anteriorly beyond the spermathecae, which is not the case with *W. clavicornis* (e.g. Fig. 278 cf. Fig. 283).



Figs. 267-272.—Male carapaces. 267, *W. auranticeps*, lateral; 268, *W. auranticeps*, in front; 269, *W. clavicornis*, type, in front; 270, *W. clavicornis*, type, lateral; 271, *W. clavicornis*, Hazen Camp specimen, in front; 272, *W. clavicornis*, Hazen Camp specimen, lateral (Scale lines 0.1 mm).

Distribution.—In N. America, this holarctic species is limited to the northern part of the continent (Map 22); there is only one record from U.S.A. It has also been recorded from east and west Greenland (Holm 1967). On at least one occasion in N. America it has been sympatric with *W. holmi*.

Natural History.—Both sexes have been taken adult in N. America in June-August; in northern Canada (Hazen Camp: Leech 1966) the species was found in cracks in the ground where the relative humidity was approaching 100%. In Greenland, the species is found amongst mosses in bogs and luxuriant heath (Holm 1967).

Walckenaeria holmi, new species

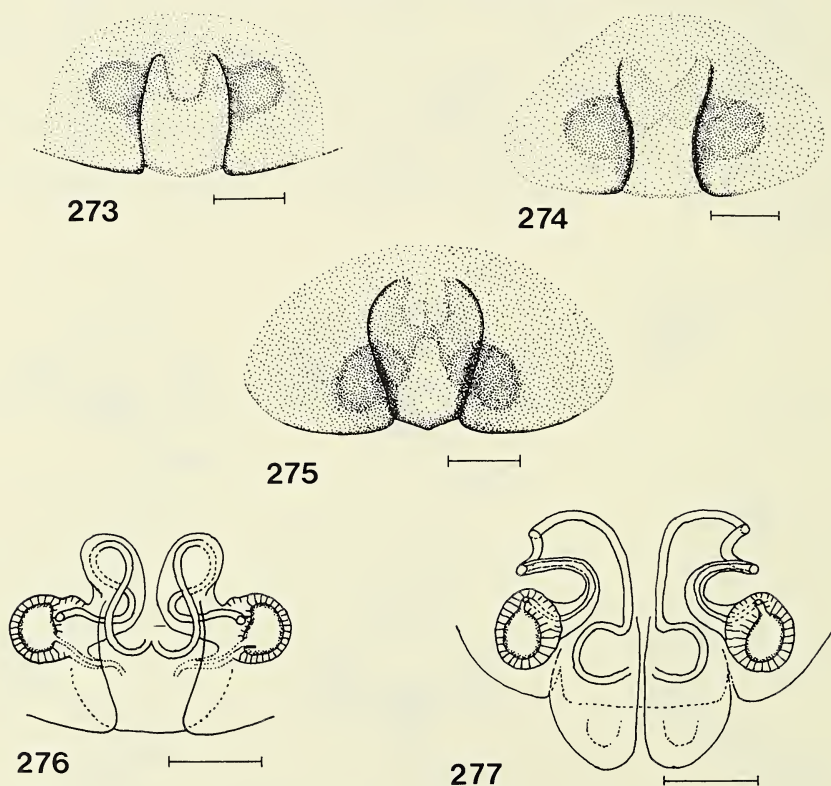
Figs. 260, 262, 265, 277, 278, 280, 282; Map 21

Cornicularia karpinskii: Holm 1967:21, and subsequent authors (misidentification: *nec* *Erigone karpinskii* O. P.-Cambridge).

Cornicularia clavicornis: Crosby and Bishop 1931: Figs. 18-22 (misidentification: *nec* *Cornicularia clavicornis* Emerton).

The species is named in honor of Dr. Å. Holm.

Type.—Male holotype from Stagg River Camp, 12 miles S.E. of Rae, Northwest Territory, 12 August 1965 (J. and W. Ivie); deposited in AMNH.

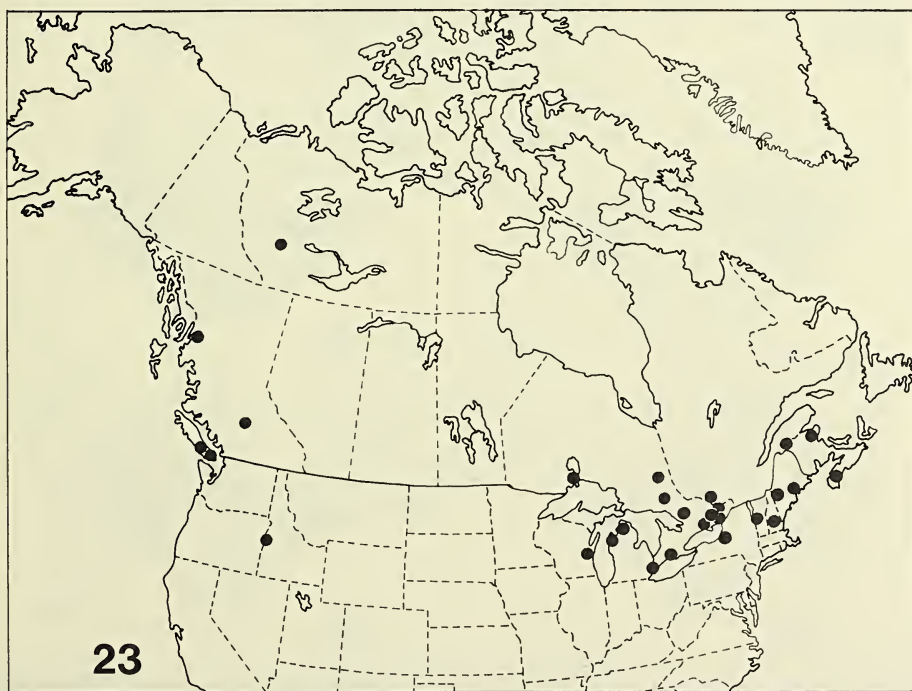


Figs. 273-277.—Epigyna, ventral. 273, *W. auranticeps*; 274, *W. lepida*; 275, *W. fusciceps*; 276, *W. auranticeps*, internal genitalia, cleared; 277, *W. holmi*, internal genitalia, cleared (Scale lines 0.1 mm).

Description.—In size, color and most other characters this species is close to *W. clavicornis*. Male palp: Figs. 260, 262, 265. Epigynum: Figs. 277, 278, 280, 282. This species has been confused in the past, both in N. America and in Europe, with *W. karpinskii* (type locality: Lake Baikal, Siberia). The male syntype of the latter species (Hope Entomological Collections, Oxford) differs from *W. holmi* in the form of the palpal tibia (Figs. 261, 264, cf. Figs. 262, 265); the distal end of the mesal apophysis is much stouter and more rounded in *W. holmi* than in *W. karpinskii*. The tibia of *W. karpinskii* seems in fact to be intermediate between those of *W. holmi* and *W. clavicornis*, with the mesal apophysis crossing the lateral apophysis much as in *W. holmi*, but with its distal end pointed as in *W. clavicornis*. The epigynum of *W. karpinskii* (female syntype) is close to that shown in Fig. 282. It is possible that *W. clavicornis* is a subspecies of *W. karpinskii*; the capture of many more examples of *W. karpinskii* would be necessary before this possibility could be properly examined. The location of the type locality makes it unlikely that this will happen.

Distribution.—This species is almost certainly holarctic in distribution; the species recorded as *W. karpinskii* in Sweden is *W. holmi*. In N. America *W. holmi* has been taken almost entirely in the more northern parts, though it occurs as far south as Wyoming in the mountains (Map 21). It has also been recorded from east and west Greenland (Holm 1967).

Natural History.—In N. America, adult females have been taken in June–September, males in June and August. Habitats were not recorded, but in Greenland (Holm 1967) the species was found amongst moss and under stones on rather moist dwarf-bush heath and in sphagnum.



Map 23.—North America. Distribution of *W. atrotibialis* (circles).

cuspidata Group

There is only one species.

Walckenaeria cuspidata brevicula (Crosby and Bishop), new status

Figs. 7, 284-291; Map 9

Walckenaera cuspidata Blackwall 1833:108.

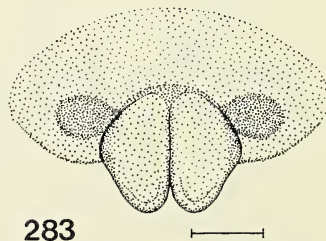
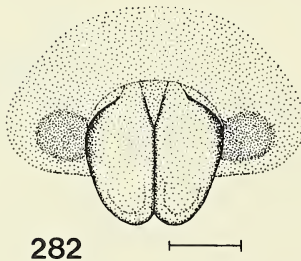
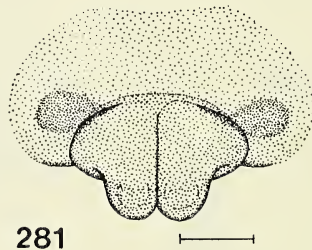
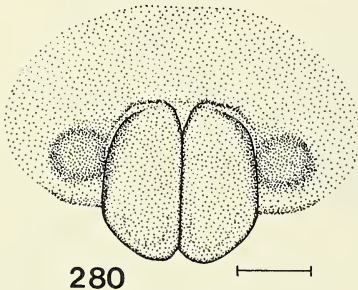
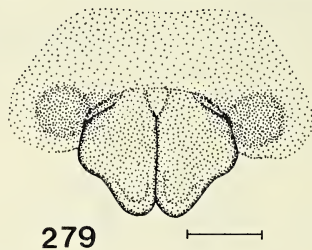
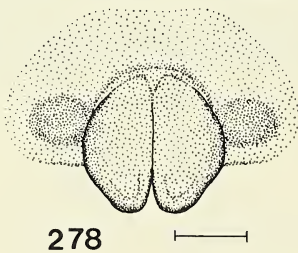
Cornicularia cuspidata: Simon 1884:844, and 1926:418, 509; Roewer 1942:660; Locket and Millidge 1953:207; Hackman 1954:62; Bonnet 1956:1221; Wiehle 1960:151.

Cornicularia brevicula Crosby and Bishop 1931:362; Roewer 1942:662; Bonnet 1956:1221; Holm 1967:27.

Walckenaeria (Heterocornicularia) cuspidata: Wunderlich 1972:389.

Types.—Blackwall's types of *W. cuspidata* are no longer in existence. The male holotype of *W. brevicula* is not in AMNH and has not been located.

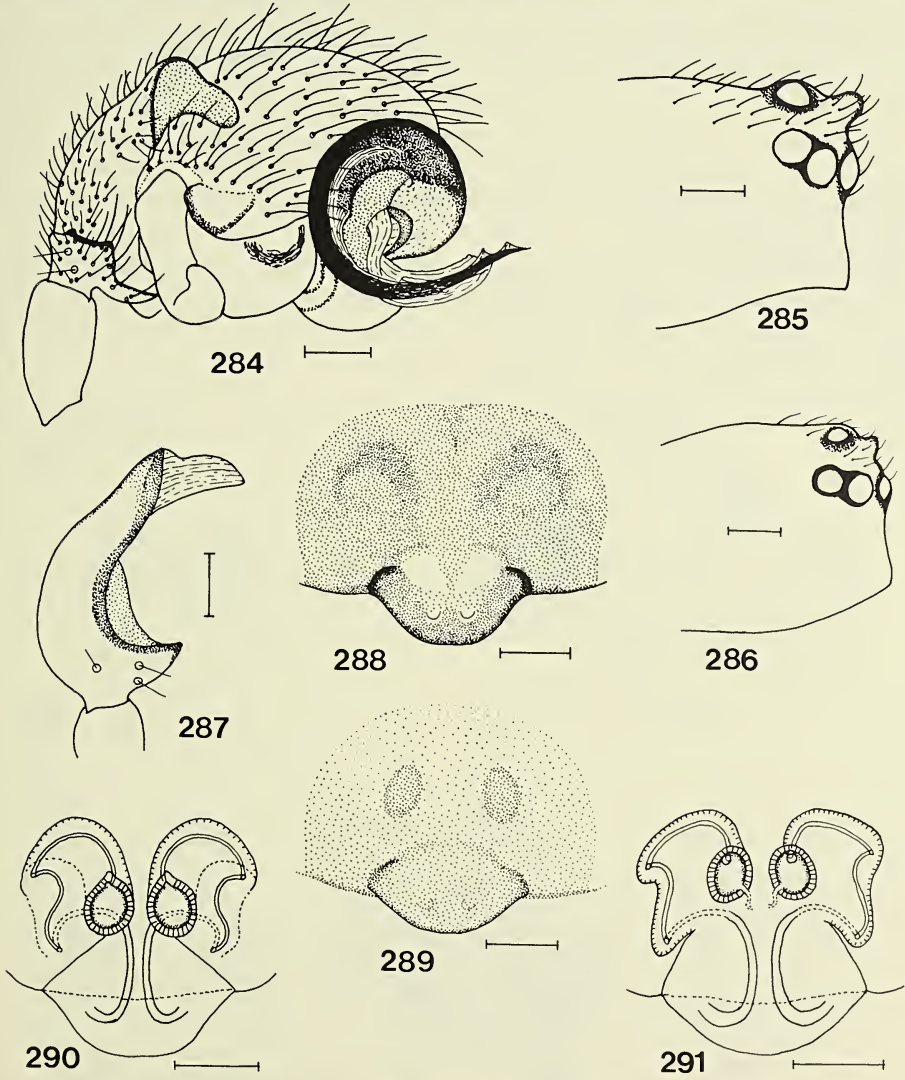
Description.—Total length: female 2.25-2.55 mm, male 2.2 mm. Carapace: length: female 1.10-1.15 mm, male 1.05 mm. Dark chestnut brown. The male has a small tubercle in the ocular area (Fig. 285); in specimens from Colorado this tubercle is



Figs. 278-283.—Epigyna, ventral. 278. *W. holmi*, New York specimen; 279, *W. clavicornis*, New Hampshire specimen; 280, *W. holmi*, Alberta specimen; 281, *W. clavicornis*, Alaska specimen; 282, *W. holmi*, Mackenzie specimen; 283, *W. clavicornis*, Hazen Camp specimen (Scale lines 0.1 mm).

minute (Fig. 286). Chelicerae: the lateral striae are fairly widely spaced in the female, less widely spaced in the male; the spacing in the female is rather wider than in European specimens. Abdomen: grey-black. Sternum: orange, suffused with black, especially on margins. Legs: pale orange to orange-brown. TmI: female 0.48-0.52, male 0.50. Male palp: Figs. 284, 287. Epigynum: Fig. 288; the spermathecae are more or less circular in outline, and usually close together (Fig. 290). In pale, presumably recently molted, females from Colorado the epigynum has a very different appearance (Fig. 289), but the internal structure (Fig. 291) shows no significant difference from that of the normal specimens.

The male palps of the N. American examples of *W. cuspidata* seem to be identical with those of the European specimens, but the females of the two populations have



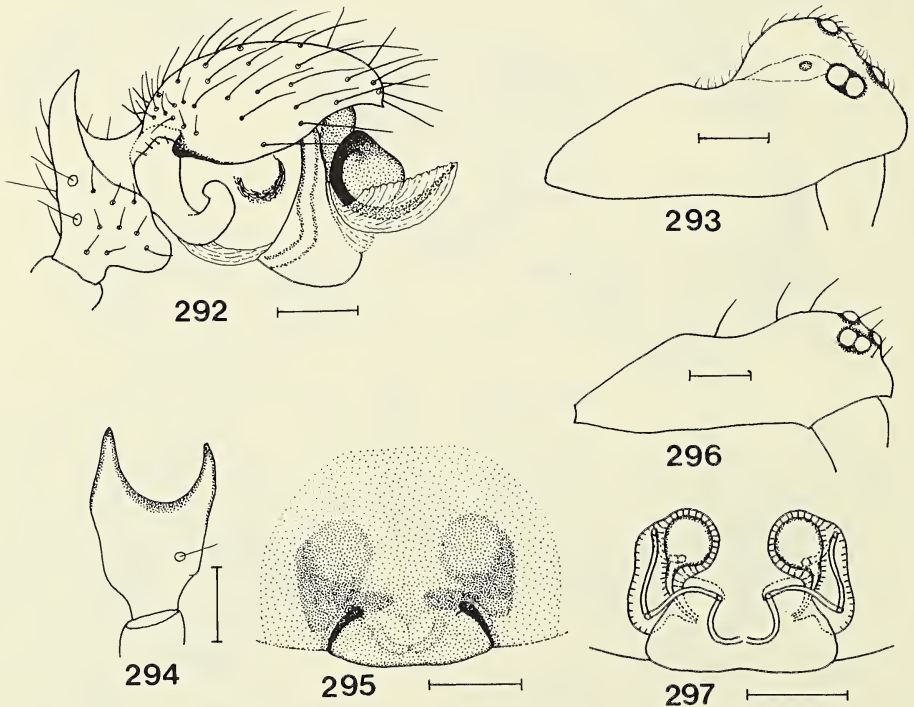
Figs. 284-291.—*W. cuspidata brevicula*. 284, male palp, ectal; 285, male carapace, lateral, Ontario specimen; 286, male carapace, lateral, Colorado specimen; 287, male palpal tibia, dorsal; 288, epigynum, usual form; 289, epigynum, Colorado specimen; 290, internal genitalia, female, cleared, Ontario specimen; 291, internal genitalia, female, cleared, Colorado specimen (Scale lines 0.1 mm).

differently shaped spermathecae. In European females the spermathecae are distinctly elongated (Figs. 301, 302), whereas in the N. American females they are rounded (Figs. 290, 291); there is some variation in the distance apart of the spermathecae, particularly in the European specimens. The cheliceral striae are somewhat more widely spaced in the American females, and the female palpal tibia is rather more swollen (as in Fig. 118, but less so) than in the European females. Because of these discrepancies, I consider it best for the present to regard the N. American population as a subspecies (*brevicula*) of *W. cuspidata*.

Diagnosis.—The male is diagnosed by the small tubercle in the ocular area (Figs. 285, 286), coupled with the form of the palp (Fig. 284) and of the palpal tibia (Fig. 287). The ocular tubercle might possibly be confused with that of *W. cornuella* (Fig. 232), but the palp of this species is quite different. The female is diagnosed by the epigynum and the internal genitalia (Figs. 288, 290), which are distinctly different from those of any other species; the possible abnormal appearance of pale specimens (Fig. 289) must be borne in mind.

Distribution.—This subspecies is probably quite widely distributed in N. America, though there are few records (Map 9). The nominate subspecies is found throughout northern and eastern Europe, and also in Siberia; the species distribution is therefore almost certainly holarctic.

Natural History.—In N. America, adult females have been taken in May, June, August and October, males in August and September. In Europe the species occupies a wide variety of habitats at ground level; the only habitat recorded in N. America is on the ground, under a board.



Figs. 292-297.—*W. atrotibialis*. 292, male palp, ectal; 293, male carapace, lateral; 294, male palpal tibia, meso-dorsal; 295, epigynum, N. American specimen; 296, female carapace, lateral; 297, internal genitalia, cleared, female, N. American specimen (Scale lines 0.1 mm, except 293, 296, 0.2 mm).

atrotibialis Group

There is only one species.

Walckenaeria atrotibialis O. P.-Cambridge

Figs. 292-297; Map 23

Walckenaeria atrotibialis O. P.-Cambridge 1878:116 (female).

Walckenaeria melanocephala O. P.-Cambridge 1881:596 (male and female).

Wideria melanocephala: Simon 1926:409, 410, 505; Locket and Millidge 1953:196; Bonnet 1959:4824; Wiehle 1960:121.

Walckenaeria (Parawideria) melanocephala: Wunderlich 1972:411.

Wideria atrotibialis: Roewer 1942:669.

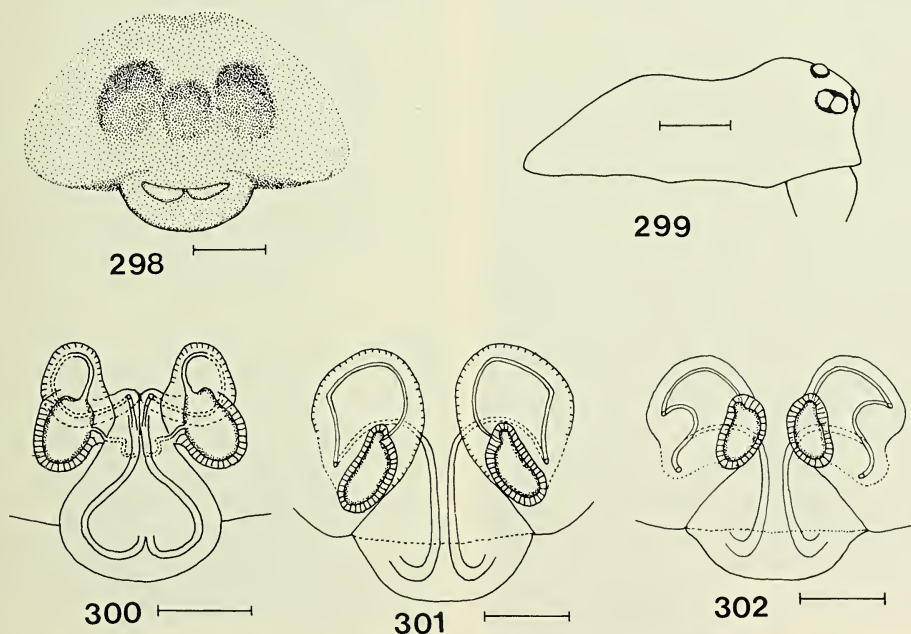
Lophocarenum abruptum Emerton 1909:189. NEW SYNONYM. This synonymy was established by examination of Emerton's male holotype (MCZ).

Mythoplastoides abruptus: Crosby and Bishop 1933:143; Kaston 1948:184.

Entelecara abrupta: Hackman 1954:63.

Type.—Female holotype in Hope Entomological Collections, Oxford (Tube No. 3500[v]); examined. As already indicated by Jackson (1916:170) and Locket (1964:262), this female is identical with the female subsequently (1881) described as *W. melanocephala*; despite the wide usage of the name *melanocephala*, the earlier name *atrotibialis* must be used.

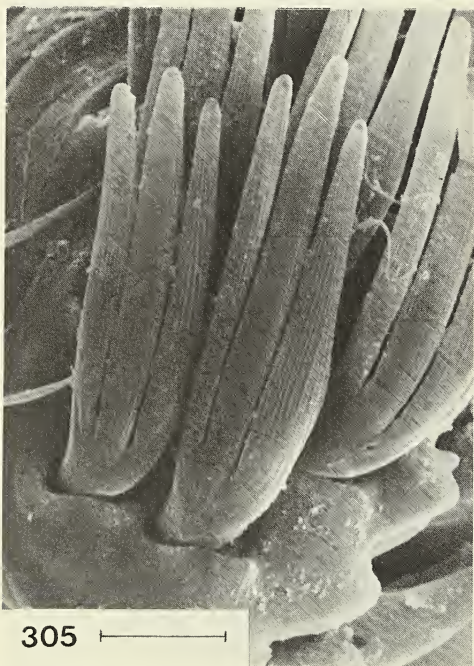
Description.—This is based on N. American specimens. Total length: female 2.5-3.1 mm, male 2.0-2.6 mm. Carapace: length: female 1.0-1.1 mm, male 0.9-1.05 mm. Orange, suffused anteriorly to a variable degree with brown; raised anteriorly in the female (Fig.



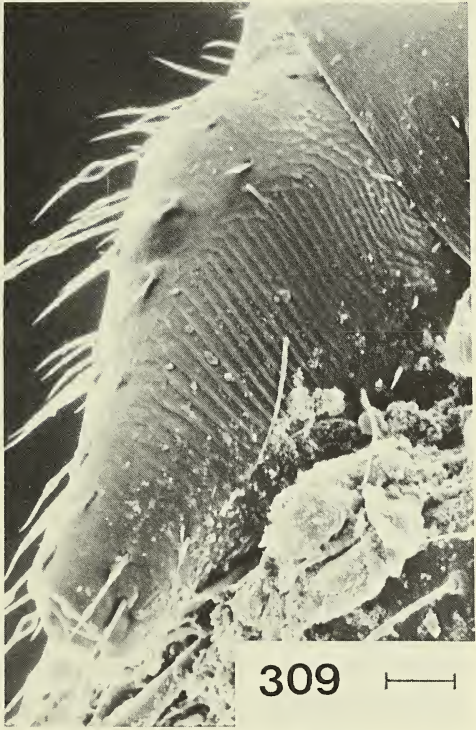
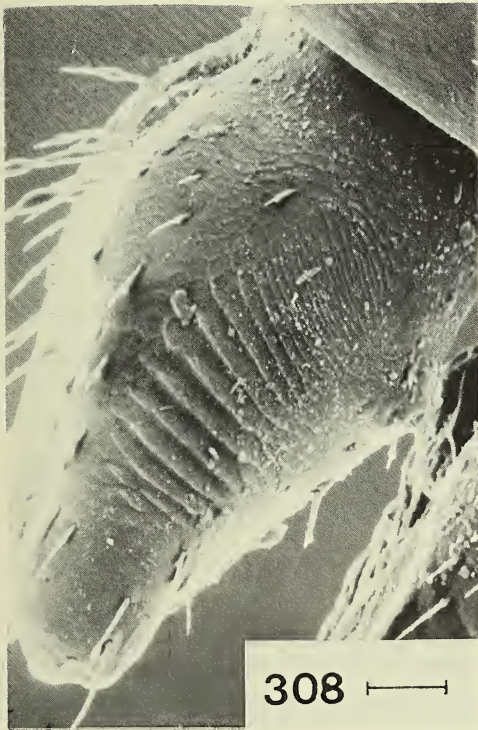
Figs. 298-302.—298, *W. fraudatrix*, epigynum; 299, *W. fraudatrix*, female carapace, lateral; 300, *W. fraudatrix*, internal genitalia, female; 301, *W. cuspidata cuspidata*, female, internal genitalia, cleared; 302, *W. cuspidata cuspidata*, female, internal genitalia, cleared, another specimen (Scale lines 0.1 mm).

296). The male has a shallow lobe with holes and sulci laterally (Fig. 293), and the clypeus projects strongly. Chelicerae: the lateral striae are well spaced in both sexes; the spacing is more or less the same as in European specimens. Abdomen: grey to black. Sternum: orange, with dusky margins. Legs: orange-brown, with femora and tibiae of legs I-II suffused with brown to deep brown. TmI: female 0.58-0.62, male 0.51-0.58. Male palp: Figs. 292, 294. Epigynum: Figs. 295, 297. The N. American specimens show only minor differences from the European specimens; the most consistent difference is that the spermathecae, though similarly shaped, are rather smaller and further apart in the American females.

Diagnosis.—The male is diagnosed by the form of the carapace (Fig. 293), coupled with the form of the palpal tibia, which has two apophyses (Fig. 294). The female is diagnosed by the epigynum (Fig. 295) and the internal genitalia (Fig. 297), both of which are quite distinct from those of other species.



Figs. 303-307.—Scanning electron micrographs. 303, *W. directa*, male horn; 304, *W. subdirecta*, male horn; 305, *W. directa*, trifurcate hairs on male horn; 306, *W. communis*, male horn; 307, *W. pallida*, lobe of male carapace (Scale lines 20 μ . except 305, 10 μ).



Figs. 308-311.—Chelicerae, lateral. 308, *W. directa*, female; 309, *W. subdirecta*, female; 310, *W. directa*, male; 311, *W. subdirecta*, male (Scale lines 40 μ).

Distribution.—This species is widely distributed in northern and eastern Europe, and in northern N. America (Map 23); it has not been recorded from Siberia. In addition to the records shown in Map 23, Hackman (1954) reported the species from Newfoundland (as *E. abrupta*).

Natural History.—In N. America, adults of both sexes have been taken in May-August. Habitats recorded are in woods, in grass, in calcareous and sphagnum bogs, in litter and in a soil sample.

antica Group

There is only one species recorded from N. America.

Walckenaeria fraudatrix, new species

Figs. 298, 299, 300; Map 8

Wideria antica: Holm 1960:124 (misidentification: *nec Theridion anticum* Wider).

Type.—Female holotype Kotzebue, Alaska, 13-14 August 1958 (C. Lindroth); deposited in MCZ.

Description.—Only the female is known. Total length: female 2.45 mm. Carapace: length: female 1.0 mm. Deep orange, suffused with chestnut brown anteriorly and on margins; carapace raised anteriorly (Fig. 299). Chelicerae: lateral striae fairly closely spaced. Abdomen: grey-black. Sternum: orange, suffused with black. Legs: orange. TmI: female 0.47. Female palp: brown, darker in color than the legs. Epigynum: Figs. 298, 300. The genitalia of this species differ from those of the known European species of this group (Wunderlich 1972; Kronstedt 1980).

Diagnosis.—This species is recognized by the epigynum (Fig. 298).

Distribution.—Known only from the type locality (Map 8).

Natural History.—The type female was taken adult in August; nothing was recorded on habitat.

ACKNOWLEDGMENTS

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OPILIONES OF THE FAMILY PHALANGODIDAE FOUND IN COSTA RICA

Clarence J. and Marie L. Goodnight

Department of Biology
Western Michigan University
Kalamazoo, Michigan 49008

ABSTRACT

Members of the opiliones family, Phalangodidae, found in Costa Rica are considered here. Previously described species were examined. Two new genera, *Costabrimma* and *Neocynorta* are defined. Species described include: *Costabrimma cruzensis*, n. sp., *C. nicoyensis*, n. sp., *C. terrena*, n. sp.; *Dapessus tarsalis* (Banks), *D. albitrochanteris* (Roewer), *D. atroluteus* (Roewer), *D. brevis* (Roewer), *D. foliatus*, n. sp., *D. gracilipes* (Roewer), *D. llorensis*, n. sp., *D. parallelus* (Goodnight and Goodnight), *D. tenuis* (Roewer), *D. trochantericus* (Roewer), *D. vitensis*, n. sp., *D. zalmoxiformis* (Roewer); *Neocynortina dixonii*, n. sp., *Pachylicus rugosus* (Banks), *P. cotoensis*, n. sp., *P. foveolatus*, n. sp., *P. hirsutus* Roewer, *P. hispidus*, n. sp., *P. spinatus*, n. sp.; *Panopiliops reimoseri* (Roewer), *P. inops*, n. sp.; *Phalangoduna granosa* Roewer; *Stygnoleptes analis* Banks; *Stygnomma fuhrmanni* Roewer and *Pellobunus insularis* Banks. All species with the exception of *Pellobunus insularis* are members of the subfamily Phalangodinae; *P. insularis* is regarded as a member of the subfamily Samoninae. All species are illustrated; keys are provided for the identification of males to most genera.

INTRODUCTION

Costa Rica, located as it is in Central America, represents an interesting area for the study of the distribution of tropical faunas. The country has an enormous variety of habitats varying from high mountains to coastal areas and from dry to moist conditions. It is an integral part of the area that formed a passage from South America to North America, possibly during Upper Cretaceous times and certainly during the Jurassic. This unique situation has made possible a fauna with at least three elements: that is, species representing invasions from South America, indigenous forms, and forms related to or derived from more northern areas.

The study of the opilionids, particularly of the phalangodids of this interesting country has not been extensive. Pickard-Cambridge (1905) did describe some opilionids from Costa Rica, but no phalangodids were included in his studies. Banks in short papers published in 1905, 1909 and 1914 described a few species. Roewer (1923) listed these forms and later (1933) listed 37 species as being from Costa Rica. In 1949 he described several more species. Of these descriptions, only a relatively few were members of the family Phalangodidae. Other workers who have described a few forms from Costa Rica include Soerensen (1932), Chamberlin (1925) and Petrunkevitch (1925). As can be easily observed, there has been no attempt to bring the information together in a single publication for easier access.

This paper is concerned with the opilionids of the family Phalangodidae which we have found to occur in Costa Rica. As was to be expected, the three types of species, as mentioned above, were encountered; members of the genus *Dapessus* (= *Cynortina*) represent a widespread genus which is found in much of Central America, probably representing forms originating north of Costa Rica. *Stygnomma fuhrmanni* Roewer represents a northern record for a species originally described from Venezuela. Of the indigenous genera, *Costabrimma* probably is the most representative.

Most of the material studied was collected by ourselves and our son, Charles, during the summers of 1976 and 1978. Unless otherwise noted, the collections cited were made by at least one of us. Charles Goodnight, alone, was responsible for the collections from the Osa Peninsula. During our two visits to Costa Rica, we attempted to visit as many different areas as possible in order to have an adequate representation of the fauna.

Collections were done by means of Berlese funnels, sifting of debris and by careful observation of overturned logs and rocks. Animals were preserved in 95% alcohol. Genitalia were mounted on slides in Turtox CM CP-9AB and observed under a compound microscope.

Whenever possible, the locality records include the name of the province in which the collection was made. Inasmuch as many of the locality records of Roewer's specimens did not indicate with any degree of exactitude where the collection took place, the record is incomplete. Every attempt was made to determine the exact locale, but many were not listed on the maps available to us. Such is also the case with Soerensen's record.

It will be noted that some of the synonymies are quite extensive. This is due to the fact that several of the species are quite variable and were unwittingly described several times by different investigators. Also Dr. Roewer, though he was usually correct in his diagnosis of new species, tended to regard each individual as a separate genus and species. This has unfortunately lead to several errors, not only on his part, but on that of ourselves and other workers. We hope that we have at least partially corrected some of the problems arising from this.

We have attempted to describe only forms of which we had both males and females. Only in one case, *Panopiliops inops*, did we set up a species based only on a female. This particular form is blind and quite unlike any other species; presumably the male would be easily recognized. In three cases [*Dapessus brevis* (Roewer), *Dapessus tenuis* (Roewer), and *Dapessus trochantericus* (Roewer)] we had only females available for study; thus the descriptions are not nearly so adequate as we would desire.

Holotypes and most paratypes of new species as well as identified forms of most species are deposited in the collections of the American Museum of Natural History, New York. We have retained a few paratypes for our own collection.

SYSTEMATICS

PHALANGODINAE ROEWER

Key for Identification of Genera, based on males

1. Tarsus I with four or more segments6
 Tarsus I with three segments2
2. Tarsal segments numbering 3-5-5-5, or 3-5-5-6, eye tubercle in the form of a forward pointing cone, often with tubercles.*Costabrimma*

- Tarsal segments somewhat more variable in number, eye tubercle with spine, low and oval in shape, or in form of low cone.3
3. Eye tubercle removed from anterior margin of cephalothorax, a low cone; male penis not sclerotized shaft, animal less than 2 millimeters in length. *Neocynortina*
Eye tubercle unlike above, low and oval, or with spine4
4. Eye tubercle with dorsal, forward pointing spine *Pachylicus*
Eye tubercle without spine5
5. Secondary sexual characters usually in form of enlarged tarsal segments; tarsal segments varying in number, 3-6 or more than 6-4 or 5, 6 *Dapessus*
Secondary sexual characters in the form of spines on leg IV and usual presence of large spine on anal operculum; tarsal segments variable in number: 3-6-4-5, 3-6-5-5, or 3-5-4-5 *Stygnoleptes*
6. Eyes present, but not on tubercle, usually directly on cephalothorax. . . . *Stygnomma*
Eye tubercle present7
7. Eye tubercle prolonged into a prominent spine *Panopiliops*
Eye tubercle rounded.8
8. Eye tubercle rounded, usually removed from the anterior margin of the cephalothorax. *Pellobunus*
Eye tubercle rounded, on anterior margin of cephalothorax. *Phalangoduna*

Costabrimma, new genus

Type species.—*Costabrimma cruzensis*, new species.

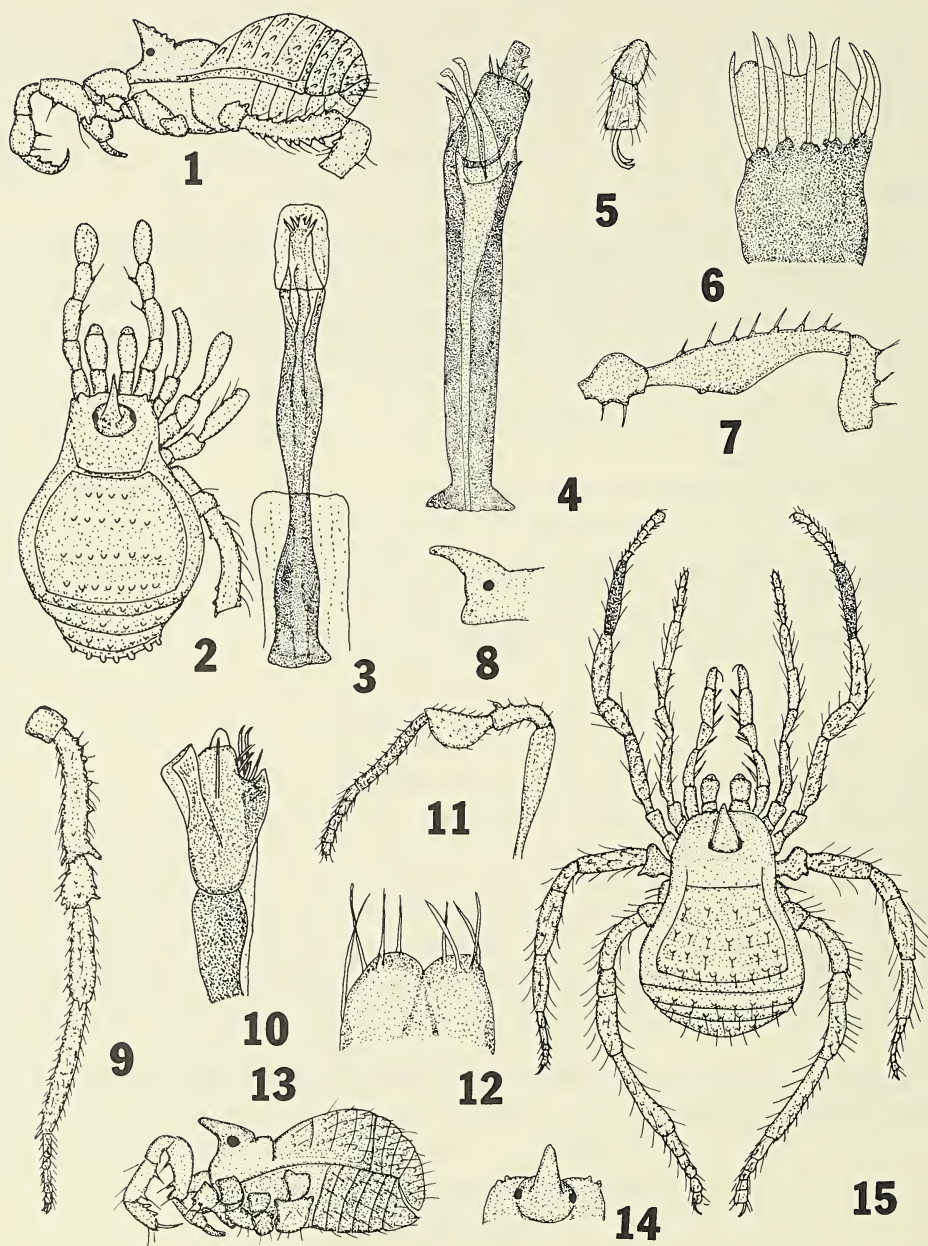
Diagnosis.—Very small forms, eye tubercle on or very close to the anterior margin of the cephalothorax, in the shape of a forward pointing cone. Five dorsal areas present, first without a median line, posterior margins parallel. Legs usually quite short; metatarsi without astraguli or calcanei. Tarsal segments 3-5-5-5 or 3-5-5-6, distitarsus of first tarsus with two segments, second with three. Double claws of tarsi III and IV simple, arising independently. Penis a sclerotized shaft; ovipositor usually bluntly rounded, with numerous setae. Secondary sexual characters variable, usually in the form of leg modifications.

Remarks.—The unusual eye tubercle and the number of tarsal segments distinguish this group from other genera.

Costabrimma cruzensis, new species
Figs. 1-7

Description of male holotype.—Total length of body, 2.9 mm; cephalothorax, 0.9 mm; width of body at widest portion, 1.9 mm. Length of Legs (I-II-III-IV in mm): Trochanter 0.2-0.3-0.2-0.4; Femur 0.9-1.0-0.9-1.1; Patella 0.4-0.4-0.3-0.5; Tibia 0.6-0.8-0.9-1.1; Metatarsus 0.8-0.8-0.9-1.1; Tarsus 0.8-1.1-0.8-1.2; Total 3.7-4.4-3.9-5.3.

Anterior margin of cephalothorax with two blunt spines on either side. Eye tubercle nearly on the anterior margin, in the form of a forward pointing cone, with several tubercles on the posterior portion, surface otherwise smooth. Each dorsal area with a transverse row of low tubercles, those of the fifth area somewhat larger. Anal operculum



Figs. 1-7.—*Costabrimma cruzensis*, new species: 1, lateral view of male; 2, dorsal view of male; 3, ventral view of penis; 4, lateral view of penis; 5, distal segments of tarsus IV of male; 6, dorsal view of distal portion of ovipositor; 7, trochanter, femur, and patella of leg II of male.

Figs. 8-15.—*Costabrimma nicoyensis*, new species: 8, lateral view of eye tubercle of male; 9, lateral view of leg IV of male; 10, lateral view of distal tip of penis; 11, lateral view of leg II of male; 12, dorsal view of distal tip of ovipositor; 13, lateral view of male; 14, dorsal view of eye tubercle of male; 15, dorsal view of male.

with similar tubercles. Spiracle partially concealed by small spines from the posterior portion of coxae IV. Coxae of legs and palpi with numerous low tuberculations, which are larger on the anterior surfaces of coxae IV. Free sternites each with a transverse row of low tubercles.

Penis a sclerotized shaft as illustrated.

Palpus: trochanter 0.3 mm long; femur, 0.5; patella, 0.3; tibia, 0.4; and tarsus, 0.4. Total length, 1.9 mm. Palpal femur and patella each with an anterior-median spine. Chelicerae not enlarged.

All segments of legs with investing hairs, low tuberculations present on all segments but the tarsi. Femur II with a proximal enlargement as illustrated, no special structural details were observed. Femur IV slightly curved. Tarsal segments 3-5-5-5.

Color a uniform yellow brown, all appendages slightly lighter, tarsi of legs nearly white.

Female.—Total length of body, 1.9 mm; cephalothorax length, 1.1 mm; width of body at widest portion 2.1 mm. Similar in appearance to male but lacking the enlarged area of leg II.

Type data.—Male holotype and male and female paratypes from Las Cruces, near San Vito, Puntarenas, 1 August 1976.

Additional records.—Limon, Siquirres, 26 July 1976, one female.

Remarks.—This species has a very distinctive eye tubercle and general appearance, easily separating it from other members of this genus.

Costabrimma nicoyensis, new species

Figs. 8-15

Description of male holotype.—Total length of body, 1.7 mm; cephalothorax length, 0.6 mm; width of body at widest portion, 1.2 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.15-0.20-0.20-0.15; Femur 0.55-0.70-0.60-0.76; Patella 0.35-0.30-0.25-0.25; Tibia 0.50-0.50-0.50-0.60; Metatarsus 0.40-0.65-0.60-0.90; Tarsus 0.40-0.60-0.40-0.45; Total 2.35-2.95-2.55-3.11.

Surface of cephalothorax smooth, eye tubercle on anterior margin, large with forward pointing spine and large eyes at base. Anterior margin of cephalothorax with rounded tubercles at the lateral margins. Abdomen rounded, broader than cephalothorax, dorsal areas indicated by transverse rows of rounded tubercles. Each free tergite with a transverse row of blunt rounded tubercles. Ventral surface relatively smooth. Coxa I and II each with a median transverse row of low tubercles which are larger at the distal portion. Coxa III with low tubercles on the anterior and posterior margins. Coxa IV with scattered tubercles which are larger on the lateral border. Each free sternite with a median transverse row of low tubercles. Anal operculum with slightly enlarged scattered tubercles. Spiracles slightly concealed.

Penis as in figure.

Palpus: trochanter, 0.15 mm long; femur, 0.3; patella, 0.1; tibia, 0.2; and tarsus, 0.2. Total length, 0.95 mm. Palpus armed as in figure. Femur with two ventral spines near the base, a single smaller spine on the outer border; a single median-apical spine on the patella; tibia and tarsus each with two spines on either side. Tarsal claw slender; chelicerae not enlarged, claws slender.

All segments of the legs with numerous hairs; trochanters rounded, trochanter III with enlarged tubercles. Femur, tibiae, and patellae of legs III and IV somewhat curved with heavier tubercles. Tibia of leg II with a ventral enlargement as in figure. Tarsal segments: 3-5-5-5.

Dorsum uniform yellow brown, appendages concolorous with dorsum; tarsi somewhat lighter; metatarsus II darker.

Female.—Total length of body, 1.75 mm; cephalothorax, 0.55; width of body at widest portion, 1.3 mm. Similar in appearance to male, but lacking the enlargement of tibia II and the small spines of leg IV.

Type data.—Male holotype, two male paratypes, one female and four immatures from Jabilla, Nicoya Peninsula, Puntarenas, 12 July 1976.

Additional records.—Guanacaste, Santa Rosa National Park, three males, one female, three immatures, 7 July 1976; Puntarenas, Nicoya Peninsula, Reserve near Cabuya, one male, 11 July 1976; Puntarenas, Nicoya Peninsula, Tambor, three males, five females, three immatures, 8 July 1976; Puntarenas, Manuel Antonio National Park, one male, two females, 21 July 1976.

Remarks.—As with other species of this genus, this form has a distinctive eye tubercle and an unusual leg enlargement.

Costabrimma terrena, new species

Figs. 16-21

Description of male holotype.—Total length of body, 2 mm; cephalothorax length, 0.75 mm; width of body at widest portion, 1.5 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.2-0.2-0.2; Femur 0.6-0.7-0.7-0.9; Patella 0.2-0.2-0.3-0.4; Tibia 0.4-0.7-0.5-0.8; Metatarsus 0.6-0.7-0.7-0.9; Tarsus 0.5-0.8-0.6-0.7; Total 2.5-3.3-3.0-3.9.

Anterior margin of cephalothorax with two blunt spines on either side. Eye tubercle only slightly removed from the anterior margin of the cephalothorax, in the form of a blunt cone with several blunt spines on the dorsal surface. Each dorsal area with a median row of low hair-tipped blunt spines. Anal operculum with numerous similar spines. Coxae with low tuberculations. Coxa II with a larger blunt spine at the posterior-lateral border; coxa IV with three blunt tubercles at the anterior margin. Genital operculum somewhat triangular in shape, spiracles nearly concealed by posterior portions of coxae IV and a series of low projections on either side of the first free sternite. Sternites each with a transverse row of low tuberculations.

Penis a sclerotized shaft, enclosing softer structures, 0.75 mm long.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.3; tibia, 0.3; and tarsus 0.3. Total length, 1.5 mm. Palpus armed as in figure. Trochanter with a few low tuberculations on all surfaces. Femur and patella each with a median apical spine. Chelicerae normal both portions of claw without teeth.

All segments of legs but tarsi with spines and hairs. Femur I with several ventral spines at the proximal third; femur and patella of leg II each with a ventral enlargement as illustrated; all segments of leg III with heavier tuberculations and low spines; leg IV likewise armed, femur somewhat curved, tibia with numerous hairs. Tarsal segments 3-5-5-6.

Color uniform yellow brown, tarsi of legs somewhat lighter.

Female.—Total length of body, 2 mm; cephalothorax length, 0.75 mm; width of body at widest portion, 1.35 mm. Similar in appearance to male, but lacking the enlarged portions of leg II. Ovipositor encircled with setae.

Type data.—Male holotype and three females paratype from La Selva, Heredia, 4 July 1976.

Additional records.—Puntarenas, Osa Peninsula, Llorona Ridge Trail, five males, four females, two immatures, 24 August 1979; Puntarenas, Coto, one male, two females, 18 February 1957 (F. Dixon).

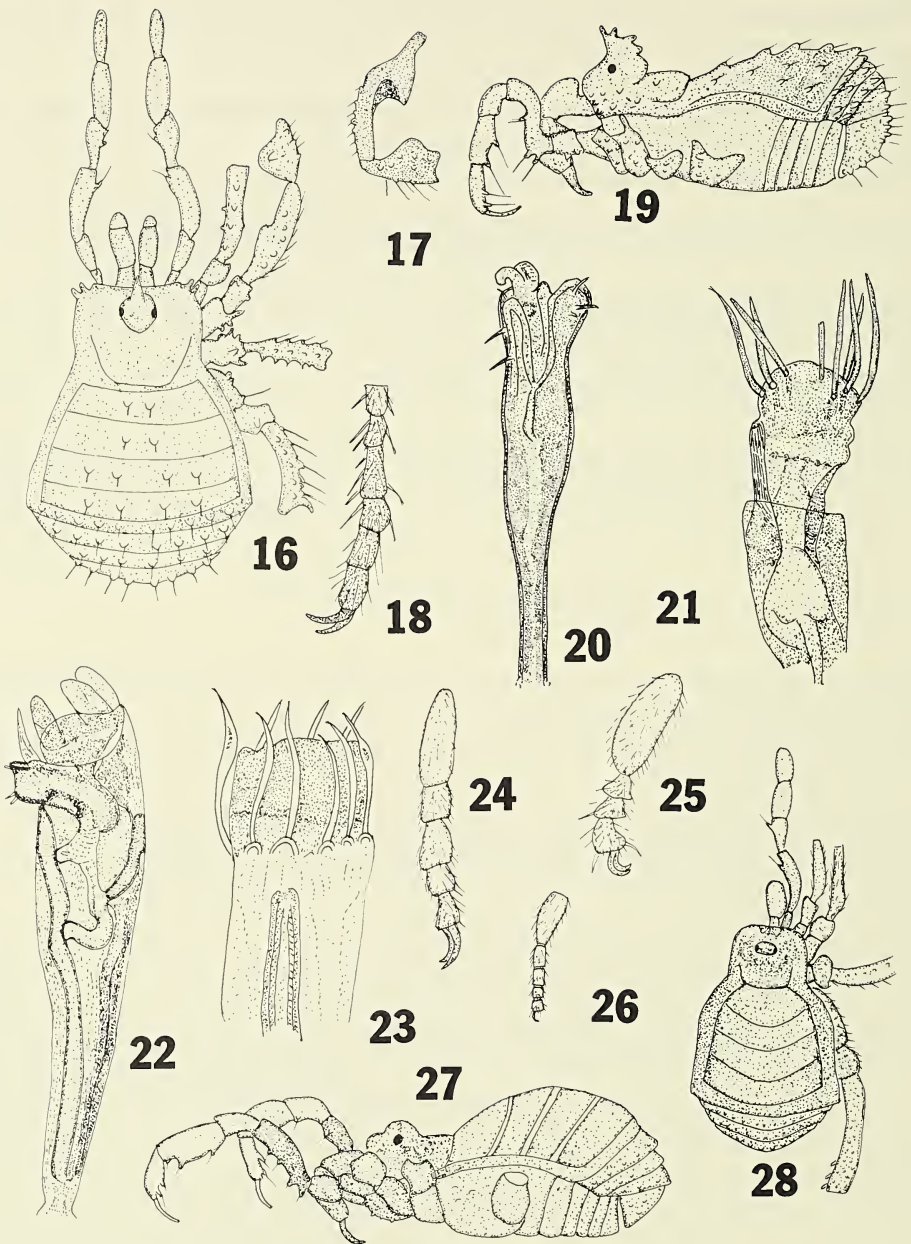
Remarks.—The unusual appearance of the eye tubercle and the enlargement of portions of leg II distinguish this species from others.

Key for the Identification of Males of the Genus *Dapessus*

- 1. Leg IV more than 14 mm long2
Leg IV less than 14 mm long4
- 2. Dorsum extremely dark, palpi lighter, contrasting*D. llorensis*
Body much lighter in color3
- 3. Abdomen arched, body more than 3 mm long, dorsal areas with transverse rows of tubercles, light reddish-yellow in color.*D. parallelus*
Abdomen not arched dorsally, body under 3 mm long, color pale yellow or reddish*D. gracilipes*
- 4. Basal segments of tarsus III enlarged5
Basal segments of tarsus III not enlarged6
- 5. Body more than 3 mm long, first two basal segments of tarsus II usually fused, thus tarsal segments appear to number 3-7-4-6.*D. tarsalis*
Body 2 mm long, with tubercles along lateral margin of abdomen and anal operculum tarsal segments 3-7-5-6*D. foliatus*
- 6. Body noticeably arched dorsally, cephalothorax narrower than abdomen.7
Body not arched dorsally, cephalothorax of same width or only slightly narrower than the abdomen8
- 7. Body over 4 mm long, dark reddish brown in color*D. zalmoxiformis*
Body less than 4 mm long, dorsal areas indicated by darker markings*D. vitensis*
- 8. Color reddish-brown, trochanters of legs, patella, tibia, and tarsus of palpus light, contrasting with dorsal portion of abdomen*D. albitrochanteris*
Color light yellow brown, dorsal areas of abdomen outlined in a somewhat darker color.*D. atroluteus*

Dapessus Roewer

Cynortina Banks 1909:228 (nec *Cynortina* Weise 1905:331); Roewer 1923:120, 1933:277; Soerensen 1932:263; Goodnight and Goodnight 1953:14.
Dapessus Roewer 1933:279.
Hewus Goodnight and Goodnight 1942a:2. NEW SYNONYMY.
Kalina Goodnight and Goodnight 1942a:2. NEW SYNONYMY.
Resinthicus Roewer 1949a:19. NEW SYNONYMY.
Parisminia Roewer 1949a:25. NEW SYNONYMY.
Sphingonus Roewer 1949a:26. NEW SYNONYMY.
Glizotus Roewer 1949a:28. NEW SYNONYMY.
Tetesia Roewer 1949a:25. NEW SYNONYMY.



Figs. 16-21.—*Costabrimma terrena*, new species: 16, dorsal view of male; 17, femur and patella of leg II of male; 18, tarsus IV of male; 19, lateral view of male; 20, lateral view of penis; 21, dorsal view of distal portion of ovipositor.

Figs. 22-28.—*Dapessus tarsalis* (Banks): 22, lateral view of penis; 23, dorsal view of tip of ovipositor; 24, tarsus of leg IV of male; 25, tarsus of leg III of male; 26, tarsus of leg III of female; 27, lateral view of male; 28, dorsal view of male.

Type species.—*Dapessus tarsalis* (Banks).

Diagnosis.—Small to medium sized animals, cephalothorax somewhat narrower than the abdomen. Eye tubercle without a dorsal spine, slightly removed from the anterior margin of the cephalothorax. Dorsal areas five in number, first area without a median line, dorsal borders of areas parallel. Free tergites smooth, spiracle usually concealed by a portion of coxa IV. Tarsal segments 3-6 or more than 6-5-6. Distitarsus of first tarsus with two segments, second with three. Metatarsi of legs without astraguli or calcanei. Tarsal claws of legs III and IV, double, smooth. Penis a chitinous shaft, usually somewhat inflated at the distal portion, enclosing softer structures. Secondary sexual characters variable, but usually consisting of enlarged basal segments of tarsus III and varying leg lengths.

Remarks.—Species of this genus are separated from one another on the basis of relative leg lengths, coloration, general body configuration, and presence or absence of various tubercles and spines.

Dapessus tarsalis (Banks), new combination
Figs. 22-28

Cynortina tarsalis Banks 1909:228.

Dapessus tarsalis Roewer 1933:279, fig. 3.

Description of male.—Total length of body, 3.3 mm; cephalothorax length 1.0 mm; width of body at widest portion, 2.4 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.5-0.5-1.2; Femur 0.9-1.6-1.3-1.2; Patella 0.5--0.8-0.5-0.9; Tibia 0.8-1.1-0.9-1.7; Metatarsus 1.2-1.4-1.2-2.0; Tarsus 0.9-1.5-1.2-1.2; Total 4.6-6.9-5.6-8.2.

Entire surface of body quite smooth; cephalothorax somewhat narrow with the eye tubercle slightly removed from the anterior margin. Two small spines present on the eye tubercle. Though the dorsal areas of most specimens were quite smooth, a few of those examined had some low tubercles at the anterior lateral border of the abdomen. Each free tergite with a transverse row of low tubercles which are slightly larger on the third free tergite. Venter relatively smooth. Coxa I with a few larger tubercles on the anterior surface, coxa IV slightly rough. Genital operculum smooth; spiracle openings partially concealed by a portion of coxa IV. Anal operculum with a few larger tubercles.

Penis a slender shaft, 1.35 mm long.

Palpus: trochanter, 0.2 mm long; femur, 0.9 patella, 0.5; tibia, 0.6; and tarsus, 0.5. Total length, 2.7 mm. Palpus armed as in figure; femur and patella each with an anterior-medial spine. Chelicerae not enlarged, normal in size.

All segments of the legs but the metatarsi and tarsi with low tubercles which are somewhat larger on the femora, patellae, and tibiae of legs III and IV, largest ones on IV. Femur IV somewhat S-shaped. Tarsal segments: 3-7-4-6 Basal segment of tarsus III enlarged. Females found with the males had the tarsal number 3-7-5-6. Careful study of late instar males revealed that the enlarged single basal segment of the male's third tarsus actually was the result of the fusion of the proximal two segments. Thus the male and female appear to have differing numbers of tarsal segments.

The entire body of most specimens studied was a deep chocolate brown, nearly black; the boundaries of the dorsal areas were somewhat lighter. In some the darker color is present as irregular markings on the cephalothorax; trochanters of legs somewhat lighter in color than the dorsum, remaining segments of the legs also lighter; chelicerae much lighter than the dorsum. Patellae, tibiae, and tarsi of palpi light yellow, contrasting

strongly with the darker color of the body. While most specimens were typically dark, a few were much redder in appearance.

Female.—Total length of body, 3.0 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 2.3 mm. Female similar in appearance to male but with five segments in tarsus III. One female examined was nearly orange in color, the legs were much darker and the palpi were conspicuously lighter. Ovipositor as figured.

Type data.—Five males and one female from La Palma (J. F. Tristan), MCZ, examined. Banks did not specify a holotype, indicating only "type" on the vial; he did not specify the location of the locality La Palma, nor did he indicate the date of collection.

Additional records.—Rio Parismina, Caribbean coast (Roewer's record), NHMS, examined (= Roewer's holotype of *D. tarsalis*.) Guanacaste, Monteverde, cloud forest, one male, three females, 26 June 1978; three males, seven females, five immatures, 27 July 1978; two males, one female 1 July 1976.

Remarks.—During the study of this genus it was pointed out that the generic name *Cynortina*, as set up by Banks and for so long recognized as a valid name actually was preoccupied. Weise, 1905, used this name; thus *Cynortina* must be replaced by the name *Dapessus* as described by Roewer, 1933. This adds another complication inasmuch as Roewer called his species *Dapessus tarsalis*, and our studies showed that Roewer and Banks had, indeed described the same animal. Roewer's name thus constitutes a homonym. Fortunately we had a considerable series of animals for our studies and were able to verify these confusing details.

Dapessus albitrochanteris (Roewer), new combination
Figs. 29-34

Cynortina albitrochanteris Roewer 1933:277.

Description of male.—Total length of body, 3.1 mm; cephalothorax length, 0.9 mm; width of body at widest point, 2.2 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.4-0.4-0.5; Femur 0.8-1.6-1.2-1.8; Patella 0.4-0.7-0.5-0.8; Tibia 0.6-1.2-0.9-1.6; Metatarsus 1.1-1.7-1.6-2.5; Tarsus 0.6-1.3-0.8-1.0; Total 3.8-6.9-5.4-8.2.

Entire dorsum with low tuberculations, eye tubercle low, rounded slightly removed from the anterior margin of the cephalothorax. Low tubercles present along the lateral border of the dorsum, terminating in slightly larger tubercles. Free tergites with only very low tuberculations; third free tergite with a pair of low spines on the posterior border. Ventral surface with scattered granulations. Coxa I with a median row of slightly larger tubercles; coxa III with a median row of teeth like tubercles at the distal portion, similar tubercles present on the posterior border, but extend over the entire length; coxa IV with slightly more conspicuous granulations. Genital operculum smooth. Free sternites and anal operculum with scattered granulations. Spiracles partially concealed.

Penis a slender shaft with a complex bifid spine at the tip, 0.9 mm long.

Palpus: trochanter, 0.3 mm long; femur, 0.5; patella, 0.3; tibia, 0.4; and tarsus, 0.4. Total length, 1.9 mm. Segments armed as in figure. Chelicera normal in size, claws smooth.

Femora, patellae, and tibiae of legs slightly enlarged; metatarsi and tarsi slender. Proximal segment of tarsus of leg III enlarged in most males examined. Tarsal segments: 3-7-5-6.

Entire dorsum and venter reddish-brown, netted with black on the cephalothorax; dorsal areas defined by darker coloration on the lateral and posterior borders. Free

tergites somewhat darker. Trochanters, particularly those of legs III and IV light, contrasting strongly with the dorsum in most specimens. Patellae, tibiae, and tarsi of palpi similarly light yellow. The proximal portion of femur IV, distal portion of tibia IV and proximal portion of metatarsus IV lighter; tarsi of legs only slightly lighter. There are slight color variations among individuals with some showing lighter colors which contrast very strongly with the dorsum.

Female.—Total length of body, 2.8 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.2 mm. Similar in appearance to male, but lacking the enlarged proximal segment of tarsus III. Ovipositor as illustrated.

Type data.—Four females, two immatures from Waldeck Farm, 45 km northwest of Limon, Limon, 15 May 1930 (Roewer's record) NHMS, examined.

Additional record.—Limon, Bomba, 21-22 July 1976, two males.

Remarks.—This animal is quite easily identified due to its distinctive coloration.

Dapessus atroluteus (Roewer), new combination

Figs. 35-38

Parisminia atroluteus Roewer 1949a;25, figs. 31a-d.

Description of male holotype.—Total length of body, 2.4 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.7 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.4-0.3-0.4; Femur 0.9-1.8-1.5-3.1; Patella 0.4-0.4-0.4-0.7; Tibia 0.7-1.6-0.9-2.8; Metatarsus 1.2-1.8-1.7-3.1; Tarsus 0.8-1.6-1.0-1.2; Total 4.2-7.6-5.8-11.3.

Entire surface of body smooth, eye tubercle low, slightly removed from anterior margin of cephalothorax, with a low raised area extending from the eye tubercle to the anterior margin. Dorsal areas clearly indicated by darker coloration, only slightly granulate. Free tergites with a few low tuberculations, otherwise smooth. Ventral surface smooth, a few fine hairs visible on coxa IV; coxa III with very low tooth-shaped tubercles on anterior and ventral surfaces. Spiracles partially concealed by coxae IV. Free sternites smooth, only a few low tubercles on the anal operculum.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.3; tibia, 0.4; tarsus 0.4. Total length, 1.7 mm. Segments armed as in figure. Femur and patella each with a median apical spine. Ventrally the femur with two proximal spines, tibia with three spines on inner surface, two on outer. Chelicera not enlarged.

All segments of legs smooth, with only an occasional low tubercle. Femur, tibia, and metatarsus of leg IV elongate. Tarsal segments: 3-7-5-6.

Entire dorsum light yellow brown, dorsal areas outlined in a somewhat darker color.

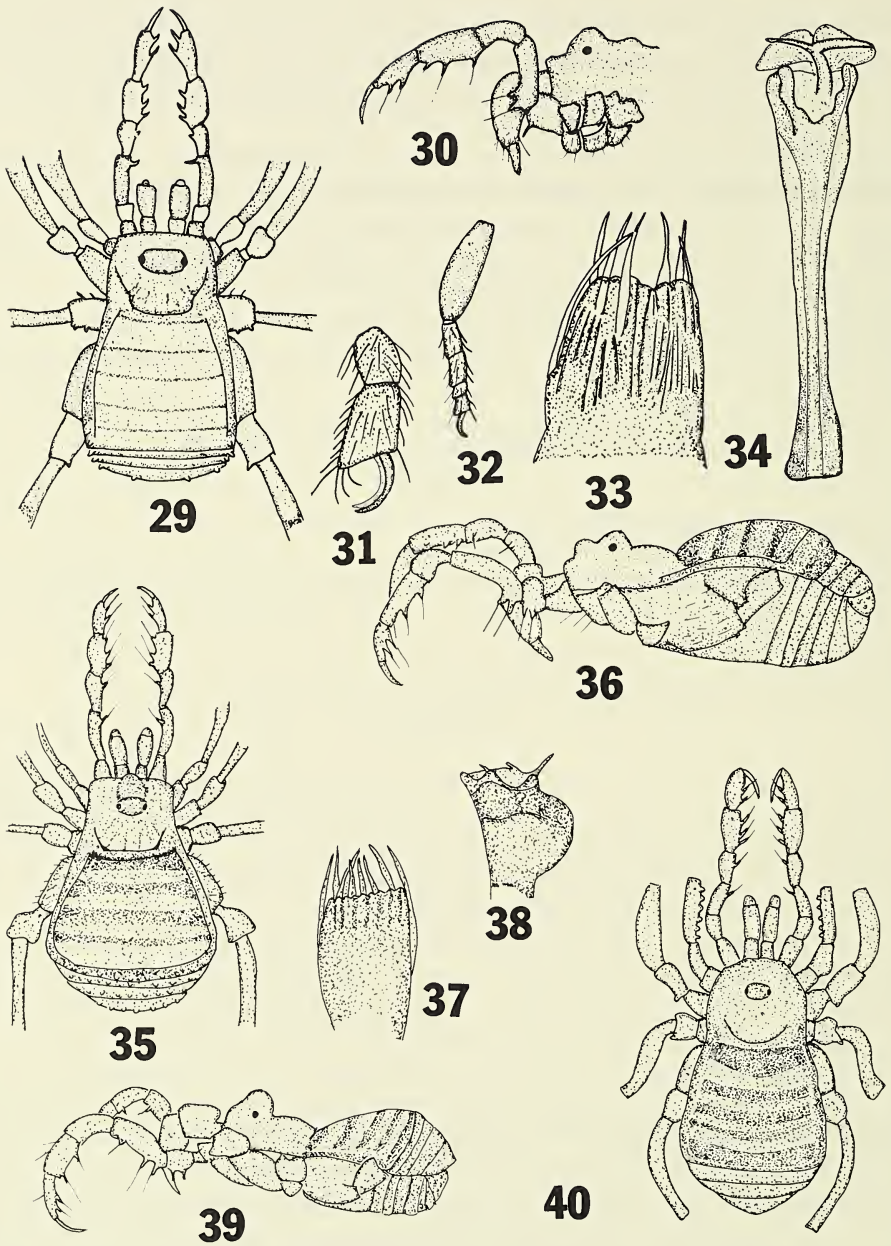
Female.—Total length of body, 2.4 mm; cephalothorax length, 0.7 mm; width of body at widest portion, 1.6 mm. Similar in appearance to male, but with femur IV somewhat shorter, S-shaped. Femora with following lengths: 0.6 mm-0.8 mm-0.7 mm-1.1 mm.

Type data.—Male holotype and female paratype from St. Clara on the Parismina River. Atlantic coast (Roewer's record) NHMS. examined.

Dapessus brevis (Roewer), new combination

Figs. 39-40

Resinthicus brevis Roewer 1949a;19, figs. 18a-d.



Figs. 29-34.—*Dapessus albitrochanteris* (Roewer): 29, dorsal view of male; 30, lateral view of cephalothorax, palpus, and chelicera of male; 31, tarsus IV of male; 32, tarsus III of male; 33, dorsal view of distal portion of ovipositor; 34, dorsal view of penis.

Figs. 35-38.—*Dapessus atroluteus* (Roewer): 35, dorsal view of male; 36, lateral view of male; 37, distal portion of ovipositor; 38, distal portion of penis.

Figs. 39-40.—*Dapessus brevis* (Roewer): 39, lateral view of female; 40, dorsal view of female.

Description of female holotype.—Total length of body, 1.75 mm; cephalothorax length, 0.6 mm; width of body at widest portion, 1.25 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.1-0.2-0.2-0.3; Femur 0.4-0.7-0.5-0.8; Patella 0.3-0.4-0.3-0.4; Tibia 0.4-0.6-0.5-0.7; Metatarsus 0.6-0.7-0.5-0.7; Tarsus 0.5-0.9-0.5-0.7; Total 2.3-3.5-2.6-3.8.

A small animal without any distinctive features; cephalothorax smooth, eye tubercle low, rounded, slightly removed from the anterior margin of the cephalothorax. Free tergites smooth. Ventral surface similarly smooth, with some hairs and low granulations on the anal operculum. Coxa IV with a short spine at the distal portion; coxa III with a few teeth on the anterior and posterior borders. Spiracle partially concealed by a portion of coxa IV.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.2; tibia, 0.3; tarsus, 0.3. Total length, 1.4 mm. Palpus armed as in figures. Femur and patella each with an apical median spine. Tibia with three spines on inner border. Chelicera small, first segment with a small dorsal enlargement.

All segments of legs with low granulations and hairs. These granulations are somewhat larger on the trochanters. Femur I with a series of low tubercles: femora III and IV slightly S-shaped. Tarsal segments: 3-6-5-6.

Entire body light reddish-brown, appendages similar in color; tarsi somewhat light.

Type data.—One female, Panzos (Roewer's record) NHMS, examined.

Remarks.—An examination of the holotype revealed that it was a female. Due to the small size and poor condition, the genitalia were not removed for detailed study.

Dapessus foliatus, new species

Figs. 41-45

Description of male holotype.—Total length of body, 2 mm; cephalothorax length, 0.6 mm; width of body at widest portion, 1.3 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.3-0.3-0.4; Femur 0.5-0.7-0.5-1.2; Patella 0.3-0.4-0.3-0.6; Tibia 0.4-0.7-0.5-1.1; Metatarsus 0.6-0.8-0.8-1.1; Tarsus 2.5-3.8-3.1-5.2. Total 2.5-3.8-3.1-5.2.

Small animal; abdomen arched, slightly wider than the cephalothorax. All dorsal surfaces smooth. Eye tubercle low, rounded, slightly removed from the anterior margin of the cephalothorax. Dorsal areas clearly defined. Lateral borders of dorsum with low spines, a similar spine present on either side of each free tergite. Dorsal portion of anal operculum with spine visible from dorsal view. Ventrally, coxal surfaces with fine granulations. Free sternites and genital operculum likewise smooth; each free sternite with a small spine on the lateral portion. Ventral portion of anal operculum with three spines. Spiracles partially concealed by low spines from the first abdominal sternite.

Penis a chitinized shaft, slightly enlarged at the distal end, 0.63 mm long.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.2; tibia, 0.3; and tarsus, 0.2. Total length, 1.3 mm. Palpus armed as in figure. Femur and patella each with a median apical spine. Chelicera normal in size, smooth.

All surfaces of legs but tarsi granulate in appearance. Femur IV curved, with spines as illustrated; tibia IV with a few low spines distally. Basal tarsal segment of leg III elongate and heavier. Tarsal segments: 3-7-5-6.

Entire animal light brownish-yellow. Dorsal areas somewhat lighter. Palpi lighter, legs nearly concolorous with the dorsum. Distal portions of tibia, metatarsus, and tarsus of leg IV lighter.

Female.—Total length of body, 2.1 mm; cephalothorax length, 1.1 mm; width of body at widest portion, 1.3 mm. Similar in appearance to male, but lacking the large spines of femur IV and the enlarged basal segments of tarsus III. Ovipositor 1.26 mm long.

Type data.—Male holotype and female paratype from Coto, Puntarenas, 17 September 1956 (E. Dixon).

Additional records.—Puntarenas, Coto, 17 September 1957 (E. Dixon), one male, two females; one male, 12 September 1957 (E. Dixon).

Remarks.—This species is quite distinctive due to the presence of spinose tubercles on the dorsum and legs.

Dapessus gracilipes (Roewer), new combination

Figs. 46-48

Tetesia gracilipes Roewer 1949a:26, figs. 35a-d.

Description of male holotype.—Total length of body, 2.5 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.65 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.4-0.4-0.4; Femur 1.6-4.1-2.5-6.3; Patella 0.4-0.7-0.5-0.6; Tibia 1.2-3.7-1.7-6.1; Metatarsus 2.4-6.0-3.3-7.6; Tarsus 1.0-2.0-1.3-1.3; Total 6.9-16.9-9.7-22.3.

A slender animal with elongated legs. Entire body, including appendages nearly smooth, with only an occasional hair, and a row of low blunt tubercles present along the lateral borders of the dorsal scute, terminating in a blunt spine at the posterior lateral border. Eye tubercle low, slightly removed from the anterior margin of the cephalothorax, a slight elevation anterior to it. Dorsal areas not clearly defined. A few very low tubercles present on the posterior border of the third free tergite; a few scattered over the anal operculum. Venter, like dorsum, smooth. Coxa I with a few low tubercles present on the median area; coxa III with low tubercles on both anterior and posterior margins. Free sternites with only a few roughened areas, spiracle concealed.

Penis a slender chitinized shaft, expanded at the distal end, 0.99 mm long.

Palpus: trochanter, 0.3 mm long; femur, 0.5; patella, 0.3; tibia, 0.4; and tarsus, 0.4. Total length, 1.9 mm. Palpus slender, armed as in figure; femur and patella each with an anterior median spine. Chelicera normal in size.

Legs extremely long and slender, all segments but trochanters and patellae much elongated. Tarsal segments: 3-7-5-6.

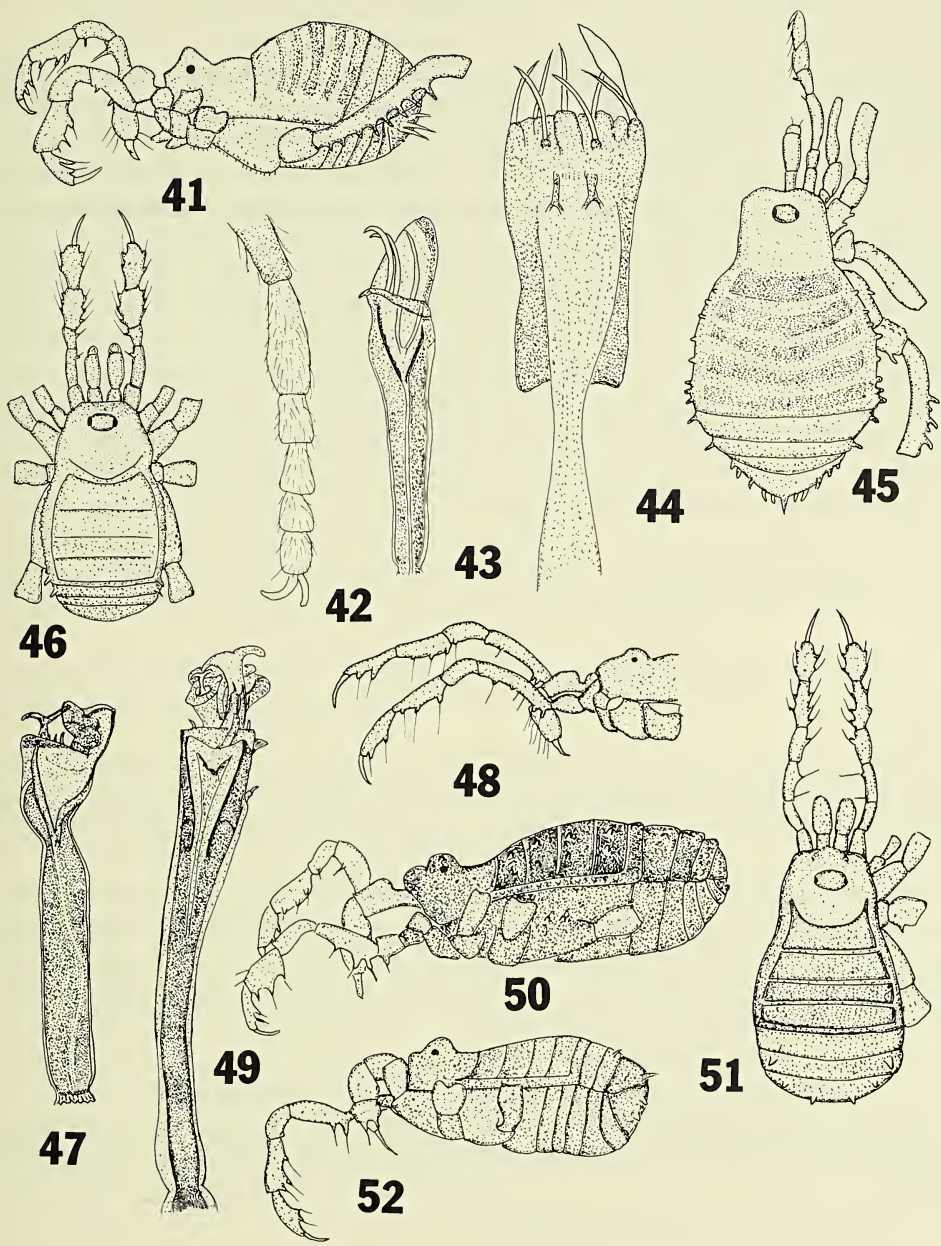
Entire body and appendages pale yellow brown.

Female.—Total length of body 2.4 mm; cephalothorax length, 0.75 mm; width of body at widest portion, 1.6 mm. Similar in appearance to male, but with shorter legs. Femora of legs with the following lengths: 1 mm-1.9 mm-1.4 mm-2.2 mm.

Type data.—Male holotype and female paratype from Tetes (Roewer's record) NHMS, examined.

Additional record.—Heredia, La Selva, one male, 6 January 1978 (O. F. Francke).

Remarks.—The specimen from La Selva differed slightly from the holotype in its coloration: it was reddish-brown with lighter palpi. Trochanter IV was also lighter, though other segments of the legs were concolorous with the dorsum. In size, this individual was slightly larger: total length, 2.8 mm; cephalothorax length, 0.8 mm; width of body at widest point, 1.7 mm. The leg lengths were as follows: 8.1 mm-21.6 mm-12.9 mm-30.8 mm.



Figs. 41-45.—*Dapessus foliatus*, new species: 41, lateral view of male; 42, tarsus III of male; 43, lateral view of penis; 44, dorsal view of ovipositor; 45, dorsal view of male.

Figs. 46-48.—*Dapessus gracilipes* (Roewer); 45, dorsal view of male; 47, lateral view of penis; 48, lateral view of cephalothorax, palpus, and chelicera of male.

Figs. 49-50.—*Dapessus llorensis*, new species: 49, lateral view of penis; 50, lateral view of male.

Figs. 51-52.—*Dapessus tenuis* (Roewer): 51, dorsal view of female; 52, lateral view of female.

Dapessus llorensis, new species

Figs. 49-50

Description of male holotype.—Total length of body, 2.7 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 1.7 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.5-0.5-0.6; Femur 2.1-5.4-3.1-5.7; Patella 0.5-0.8-0.5-1.1; Tibia 1.5-5.4-2.1-6.8; Metatarsus 2.8-9.3-3.5-8.7; Tarsus 1.0-2.1-1.4-1.7; Total 8.2-23.5-11.1-24.6.

Dorsal body surface roughened in appearance. Eye tubercle low, slightly removed from the anterior margin of the cephalothorax, with two very low tubercles above. Abdominal areas not well defined. Each area with a transverse row of slightly enlarged tubercles, a row of low tubercles on each lateral margin. Each free tergite with a transverse row of slightly enlarged tubercles, larger ones on the outer border. Anal operculum with a few enlarged tubercles. Third free tergite with two much larger spines. Free sternites smooth; coxae with very fine granulations. Coxa III with a few tooth-like tubercles on the posterior surface; coxa IV with a few larger granulations visible from dorsal view, with a ventro-posterior blunt spine which partially conceals the spiracle, genital operculum smooth.

Penis is a slender sclerotized shaft, 0.96 mm long.

Palpus: trochanter, 0.3 mm long; femur, 0.8; patella, 0.4; tibia, 0.4; and tarsus, 0.4. Total length, 2.3 mm. Palpus armed as in figure. Femur and patella each with an anterior-medial spine. Tibia with three spines on either side; tarsus with two. Chelicera normal in size.

All segments of legs smooth; trochanter III with a low spine at the posterior-proximal position; femur I with a few spinose tubercles on the ventral surface. Tarsal segments: 3-8-5-6.

Entire animal very dark brown, nearly black, giving it a very distinctive appearance. Palpi much lighter, contrasting strongly with the dorsum. Chelicerae also light in color, but somewhat darker than the palpi. All leg segments dark brown, slightly lighter than the dorsum.

Female.—Total length of body, 3.5 mm; cephalothorax length, 1.2 mm; width of body at widest point, 2.2 mm. Similar in appearance to male, but with slightly shorter legs. The legs measure: 5.3 mm-11.7 mm-8.9 mm-12.3 mm. Ovipositor with numerous setae.

Type data.—Male holotype, one male paratype, and two female paratypes from Sirena, Osa Peninsula, Puntarenas, 24 August, 1979.

Additional records.—Puntarenas, Osa Peninsula, Llorona, 9 August 1978, four males, four females; Llorona Swamp Trail, 23 August 1979, one male, one female.

Remarks.—In color, this form resembles *D. tarsalis*, but it has tubercles on the dorsum and the dorsal areas are not slightly bowed as in *D. tarsalis*. The penes are quite different distally.

Dapessus parallelus (Goodnight and Goodnight), new combination

Figs. 53-56

Kalina parallelus Goodnight and Goodnight 1942a:3, figs. 14-15.

Description of male.—Total length of body, 3.2 mm; cephalothorax, 1 mm; width of body at widest portion, 2.5 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.4-0.4-0.5; Femur 1.1-2.1-2.0-5.3; Patella 0.5-1.0-0.7-1.4; Tibia 1.9-1.6-1.5-4.5; Metatarsus 1.6-2.3-2.6-6.1; Tarsus 0.7-1.5-0.9-1.3; Total 6.1-8.9-8.1-19.1.

Entire body smooth. Eye tubercle removed from the anterior margin of the cephalothorax, two very small spines at the anterior-lateral margin of the cephalothorax. Each dorsal area with a transverse row of very low tubercles. Free tergites smooth, third with a very low tubercle at the posterior lateral margin. Venter likewise smooth. Coxa III with a few low teeth on the anterior and posterior borders. Other coxal surfaces smooth. Free sternites smooth with only a few very low tubercles at the lateral margins. Anal operculum smooth, spiracle concealed slightly by coxa IV.

Penis as illustrated.

Palpus: trochanter, 0.3 mm long; femur, 0.6; patella, 0.3; tibia, 0.5; and tarsus, 0.5. Total length, 2.2 mm. Palpal surface with fine hairs, spines as in figure. Femur and patella each with a median-apical spine; tibia and tarsus each with two large and one small spine on either side.

Legs with all segments very smooth; trochanters with a few low tubercles, remaining segments clothed only with scattered fine hairs. Tarsal segments: 3-7-5-6.

Color of entire body light reddish-yellow, trochanters of legs slightly lighter, remainder of appendages concolorous with the dorsum.

Type data.—Male holotype and male paratype from Port Limon, Limon, 25 March, 1905 (F. C. Paulmeier) AMNH, examined.

Dapessus tenuis (Roewer), new combination

Figs. 51, 52

Glizotus tenuis Roewer 1949a:28, figs.38a-e.

Description of female holotype.—Total length of body, 2.7 mm; cephalothorax length, 0.8 mm; width of body at widest point, 1.7 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.3-0.3-0.3; Femur 0.9-2.1-1.3-2.5; Patella 0.6-0.4-0.6-0.7; Tibia 0.8-1.6-1.0-1.8; Metatarsus 1.3-2.1-1.6-1.3; Tarsus 0.7-1.0-1.0-2.1; Total 4.6-7.5-5.8-8.7.

Dorsum smooth. Eye tubercle slightly removed from the anterior margin of the cephalothorax, low, rounded above. Dorsal areas smooth, free tergites likewise smooth, third with four spines, central ones slightly larger than lateral ones. Ventral surfaces smooth, with some scattered hairs. Coxa III with a few low teeth on the anterior and posterior surfaces; free sternites smooth; anal operculum with paired tubercles. Spiracle concealed.

Ovipositor with numerous setae.

Palpus: trochanter, 0.3 mm long; femur, 0.6; patella, 0.3; tibia, 0.4; and tarsus, 0.4. Total length, 2 mm. Palpus armed as illustrated. Femur and patella each with an apical median spine. Chelicera normal in size, smooth.

Legs having the femora, patella, and tibiae, slightly roughened. Tarsal segments 3-8-5-6.

Color of animal a uniform yellow brown; chelicerae and palpi somewhat lighter; trochanters of legs slightly lighter than dorsum, remainder of legs concolorous with the dorsum.

Type data.—Female holotype from Waldeck Farm, 45 km NW of Limon, Limon (Roewer's data), NHMS, examined.

Remarks.—Unfortunately there was but a single female available for study; thus the description is not entirely adequate for accurate identification of this form.

Dapessus trochantericus (Roewer), new combination

Figs. 57, 58

Parisminia trochantericus Roewer 1949a:25, figs. 33a-f.

Description of female holotype.—Total length of body, 1.8 mm; cephalothorax length, 0.6 mm; width of body at widest portion, 1.3 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.2-0.2-0.2; Femur 0.5-1.3-0.6-0.9; Patella 0.3-0.4-0.3-0.4; Tibia 0.4-0.7-0.5-0.7; Metatarsus 0.6-0.8-0.7-0.9; Tarsus 0.4-0.9-0.5-0.6; Total 2.4-4.3-2.8-3.7.

Entire dorsum and free tergites smooth. Eye tubercle low, rounded dorsally, removed from the anterior margin. Dorsal areas indicated clearly by darker markings. Venter smooth, with some very low granulations. Coxa III with anterior and posterior rows of blunt teeth. Free sternites smooth, a few low tubercles on the anal operculum. Spiracles partially concealed by portions of coxae IV.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.3; tibia, 0.3; and tarsus, 0.2. Total length, 1.4 mm. Palpus armed as in figure, chelicera not enlarged.

All segments of the legs with scattered hairs; tarsi with granulations. Tarsal segments: 3-7-5-6.

Entire animal light yellow brown; dorsal areas slightly darker; appendages lighter.

Type data.—Female holotype from Rio Parismina on the Atlantic Coast (Roewer's data), NHMS, examined.

Remarks.—In the original description Roewer indicated that the holotype was a male; unfortunately, it is a female. Inasmuch as there was but a single specimen in relatively poor condition it was impossible to study the genitalia without totally destroying the animal. Because of the sexual dimorphism so often present among the species of this genus, it is extremely difficult to be certain of the characters of the species from the examination of a single female. Possibly this species is a synonym of *D. atroluteus* (Roewer).

Dapessus vitensis, new species

Figs. 59-62

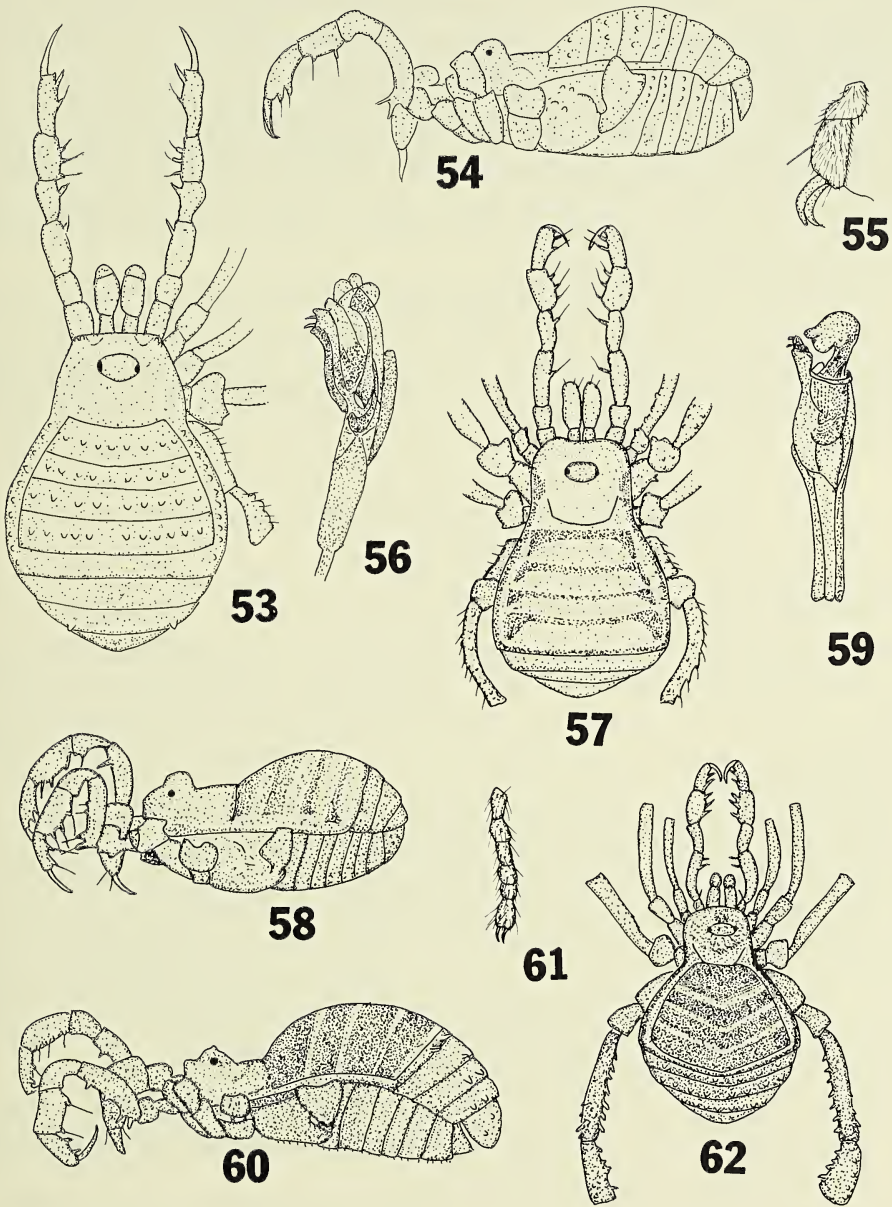
Description of male holotype.—Total length of body, 3.5 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 2.5 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.4-0.4-0.6; Femur 0.9-2.2-1.1-1.9; Patella 0.4-0.7-0.4-0.8; Tibia 0.7-1.1-1.6-1.1; Metatarsus 0.9-1.6-1.3-2.1; Tarsus 0.6-1.1-1.9-1.1; Total 3.7-7.1-5.8-7.6.

Cephalothorax much narrower (1.1 mm) than the abdomen. Abdomen arched; surface of both cephalothorax and abdomen smooth, with some small low tuberculations. Eye tubercle low, smooth, slightly removed from the anterior margin of the cephalothorax. Dorsal areas clearly indicated. Fifth area and each free tergite each with a transverse row of low spinose tubercles. Venter smooth, covered with fine hairs. Coxa of palpus with a few low tubercles; coxa III with a few tubercles on both anterior and posterior borders. Coxa IV smooth, slightly concealing the spiracle. Free sternites slightly roughened; dorsal portion of anal operculum with some low tubercles.

Penis a sclerotized shaft, dilated at apical portion, 1.29 mm long.

Palpus: trochanter, 0.2 mm long; femur, 0.5; patella, 0.4; tibia, 0.4; tarsus, 0.5. Total length 2 mm. Palpus armed as in figures. Femur and patella of palpus each with a median apical spine. Chelicera normal in size.

All segments of legs but tarsi with very low tubercles and numerous hairs. Femora, tibiae, and patellae rounded; metatarsi slender. Tarsal segments: 3-7-5-6.



Figs. 53-56.—*Dapessus parallelus* (Goodnight and Goodnight): 53, dorsal view of male; 54, lateral view of male; 55, distal segments of tarsus of leg IV of male; 56, distal portion of penis.

Figs. 57-58.—*Dapessus trochantericus* (Roewer): 57, dorsal view of female; 58, lateral view of female.

Figs. 59-62.—*Dapessus vitensis*, new species: 59, distal portion of penis; 60, lateral view of male; 61, tarsus of leg IV of male; 62, dorsal view of male.

Color of dorsum, venter, and femora, patellae, tibiae, and metatarsi of legs uniform dark reddish-brown. Tarsi of legs and tibiae and tarsi of palpi lighter. Dorsal areas black, some darker pencillings present on the cephalothorax, chelicerae, and femora of palpi.

Female.—Total length of body, 3.2 mm; cephalothorax length, 0.7 mm; width of body at widest portion, 1.7 mm. Similar to male in appearance.

Type data.—Male holotype, 3 male, 2 female paratypes, and several immature specimens from Las Cruces, near San Vito, Puntarenas, 1 August 1976.

Additional record.—Cartago, San Cristobal, 5300 feet altitude on Pan American Highway, 24 July 1976, two females.

Remarks.—In general appearance, this species is close to *Dapessus zalmoxiformis* (Roewer), but differs in color and size.

Considerable variation existed among some males, for some had more numerous spinous tubercles on the third free tergite and anal operculum than did the holotype. There was also some slight variation in the number of tarsal segments. A few females numbered 3-8-5-6. Immature forms typically had an arolium on the tarsi of legs III and IV.

Dapessus zalmoxiformis (Roewer), new combination

Figs. 63-65

Sphingonius zalmoxiformis Roewer 1949a:26, figs. 37a-d.

Description of male holotype.—Total length of body, 4.5 mm; cephalothorax length, 1 mm; width of body at widest portion, 3.2 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.6-0.6-0.8; Femur 1.2-1.9-1.5-2.6; Patella 0.6-0.8-0.7-1.2; Tibia 0.9-1.5-1.2-2.6; Metatarsus 1.3-2.0-1.7-3.1; Metatarsus 1.3-2.0-1.7-3.1; Tarsus 0.9-1.3-1.3-1.3; Total 5.2-8.1-7.0-11.6.

Body arched, surfaces smooth, cephalothorax somewhat narrower than abdomen. Eye tubercle low, rounded above. Anterior margin with a few low tubercles at the anterior lateral border. Dorsal areas clearly defined, areas with a few low scattered tubercles which are more evident on the fifth area. Each free tergite with a transverse row of very low tubercles. Numerous fine hairs present on the ventral surface, most evident on coxa IV. Coxa I with a few low tubercles; coxa II with both an anterior and posterior row of low teeth; coxa IV smooth. Spiracle partially concealed. Each free sternite with a transverse row of low tubercles. Anal operculum with a few enlarged tubercles.

Penis a chitinized shaft, enlarged at distal tip, 1.5 mm long.

Palpus: trochanter, 0.3 mm long; femur, 0.9; patella, 0.4; metatarsus, 0.7; and tarsus, 0.5. Total length, 2.8 mm. Palpus armed as in figure; femur and patella each with an anterior median spine. Chelicera normal in size.

All segments of legs except leg IV only slightly roughened. Trochanter III with a few tubercles on the posterior surface. Femur IV somewhat S-shaped, with numerous low tubercles which are somewhat enlarged toward the distal portion. Patella IV with numerous slightly enlarged tubercles; similar tubercles present on the tibia and metatarsus. Tarsal segments: 3-7-5-6.

Color dark reddish-brown, palpi and chelicerae much lighter; leg IV much darker.

Type data.—Male holotype from San Jose, San Jose (Roewer's data), NHMS, examined.

Neocynortina, new genus

Type species.—*Neocynortina dixon*i, new species.

Diagnosis.—A very small animal, body somewhat ovoid, with five dorsal areas, first without median line, borders parallel. Eye tubercle in the form of a cone, slightly removed from the anterior margin of the cephalothorax; spiracle visible, but not widely expanded. Tarsal segments: 3-6-5-6. Distitarsus of first tarsus with two segments, second with three. Double claws of legs III and IV arising independently, smooth. Metatarsi without astraguli or calcanei. Penis of male rounded, chitinized.

*Neocynortina dixon*i, new species
Figs. 66-69

Description of male holotype.—Total length of body, 1.6 mm; cephalothorax length, 0.5 mm; width of body at widest portion, 1.1 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.1-0.2-0.2-0.2; Femur 0.4-0.6-0.5-0.6; Patella 0.2-0.3-0.2-0.3; Tibia 0.3-0.4-0.4-0.5; Metatarsus 0.3-0.4-0.4-0.5; Tarsus 0.4-0.7-0.4-0.6; Total 1.7-2.6-2.1-2.7.

A small form, body somewhat ovoid in shape, eye tubercle only slightly removed from the anterior margin of the cephalothorax, somewhat cone-shaped with eyes at base. Surface of dorsum, free tergites, and venter with low tuberculations. Dorsal areas poorly defined. Surfaces of coxae and genital operculum with low granulations. Coxa II with a few posterior tubercles; coxa III with some low teeth on both anterior and posterior margins. Posterior margin of coxa IV with a few heavier granulations on the anterior surface. Spiracles visible, but not widely expanded.

Penis as illustrated, 0.4 mm long.

Palpus: trochanter, 0.15 mm long; femur, 0.45; trochanter, 0.25; tibia, 0.35; and tarsus, 0.3. Total length, 1.5 mm. Palpus armed as in figure; inner surface of femur with a single median and a single apical spine; patella with a single apical spine. Tibia with one median and one apical spine; tarsus with two spines on either side. Chelicera normal in size, first segment smooth above, second with numerous hairs.

All segments of legs but tarsi with low granulations, some hairs present. Femur IV slightly curved. Tarsal segments 3-6--5-6.

Body and appendages light brown-yellow, tarsi slightly lighter.

Female.—Total length of body, 1.6 mm; cephalothorax length, 0.5 mm; width of body at widest portion, 1.1 mm. Female similar to male in appearance, with little or no sexual dimorphism. Ovipositor bilobed, with several setae.

Type data.—Male holotype and female paratype from Coto, Puntarenas, 19 July 1957 (F. Dixon).

Additional record.—Puntarenas, Golfito, 27 August 1957 (F. Dixon), one female.

Key to the Identification of males of the genus *Pachylicus*

- 1. Leg IV more than 15 mm long *P. rugosus*
Leg IV less than 15 mm long 2
- 2. Surface of body with numerous spine-like hairs, covering all surfaces, including legs *P. hispidus*
Surfaces of body without such spine-like hairs 3

3. Spines present on the femora of legs I, II, and IV, dorsal areas of abdomen with transverse rows of hair-tipped spines *P. spinatus*
Only low tubercles present on femora, dorsum without conspicuous rows of hair-tipped spines 4
4. Dorsum with transverse rows of tubercles, median ones larger; tarsus of palpus with conspicuous fleshy protuberance *P. cotoensis*
Dorsum with less conspicuous tubercles, no protuberance on tarsus of palpus 5
5. Metatarsus of leg IV curved, with small spine at distal end. *P. hirsutus*
Metatarsus of leg IV not curved, but enlarged distally. *P. foveolatus*

Pachylicus Roewer

Metapachylus: Banks 1909:230 (nec *Metapachylus* Bates, 1889).

Parmitraceras Roewer 1912:155 (in part).

Pachylicus Roewer 1923:118.

Mexscotolemon Goodnight and Goodnight 1942c:3; 1942d:1.

Brimma Roewer 1949a:19.

Cerroa Roewer 1949a:25.

Type species.—*Metapachylus rugosus* Banks.

Diagnosis.—Small to medium sized opilionids with somewhat rounded bodies. Cephalothorax only slightly narrower than the abdomen. Eye tubercle slightly removed from the anterior margin of the cephalothorax, with a median spine. In most species, this spine is strongly curved forward. The five dorsal areas are clearly defined, first without a median line, dorsal borders parallel, often with spines or tubercles. Free tergites often with spines; free sternites usually smooth. Spiracles usually concealed by some portion of coxa IV.

Tarsal segments: 3-6 or more than 6-5-5- or 6. Distitarsus of first tarsus with two segments, second with three. Metatarsi not divided into astraguli or calcanei. Tarsal claws of legs III and IV double, smooth, arising independently. Penis a chitinous shaft, usually somewhat inflated at the tip, softer portions varying in appearance. Secondary sexual characters variable, usually involving longer legs in the male or varying degrees of spination on the third and fourth legs.

Remarks.—Species are separated from one another on the basis of the form of the eye tubercle, the spination of the dorsum, coloration of the body, and secondary sexual characters.

Pachylicus rugosus (Banks)

Figs. 70-72

Metapachylus rugosus Banks 1909:230.

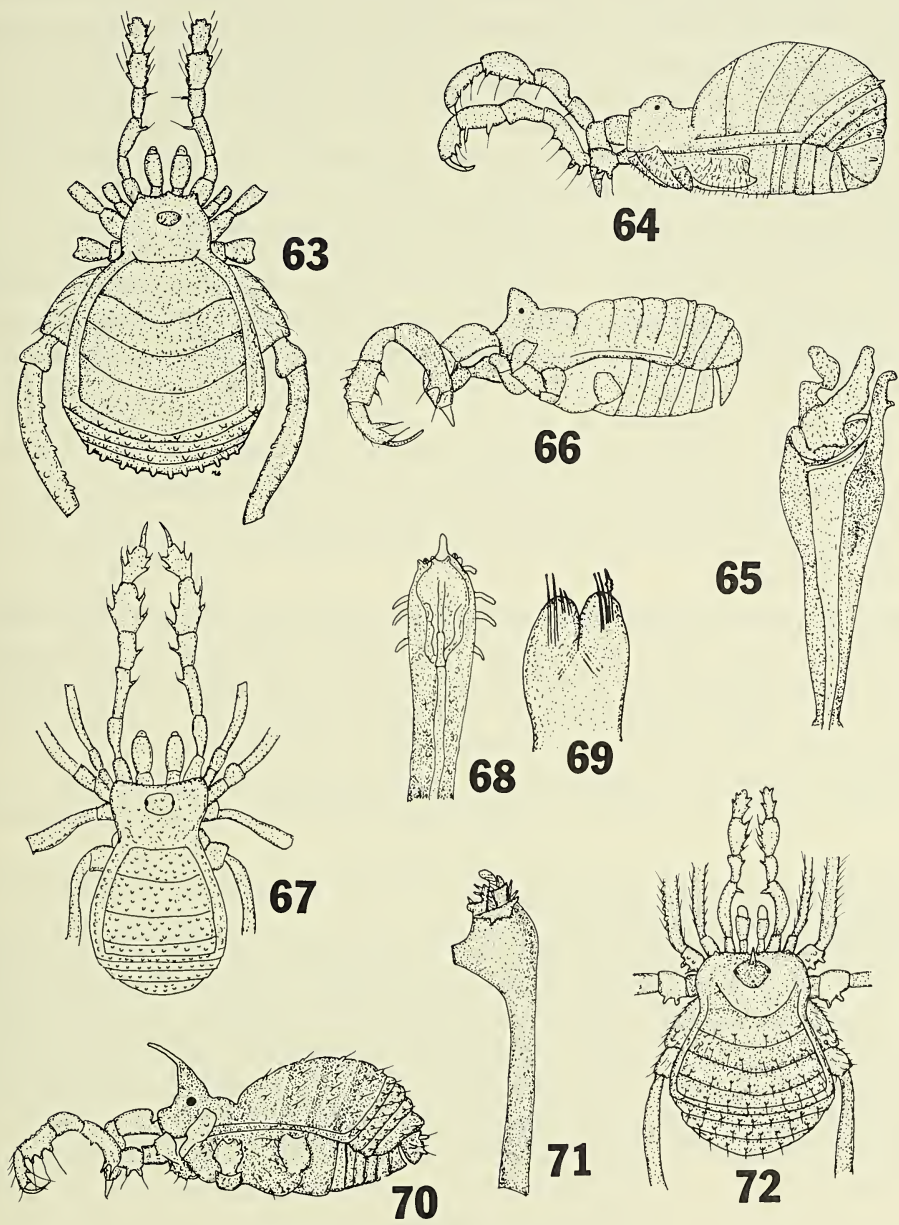
Parmitraceras rugosus: Roewer 1912:155.

Pachylicus rugosus: Roewer 1923:118, fig. 121.

Mexscotolemon insularis Goodnight and Goodnight 1942c:3, figs. 1-4. **NEW SYNONYMY.**

Cerroa hirsuta Roewer 1949a:25, figs. 34a-f. **NEW SYNONYMY.**

Description of male.—Total length of body, 4.3 mm; cephalothorax length, 1.3 mm; width of body at widest portion, 3.3 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.6-0.6-0.6-0.8; Femur 3.0-2.9-2.4-6.4; Patella 0.8-1.1-0.8-1.9; Tibia 1.3-2.4-1.9-6.2; Metatarsus 2.1-3.2-3.0-6.9; Tarsus 1.1-2.1-1.6-1.3; Total 8.9-12.3-10.3-23.5.



Figs. 63-65.—*Dapessus zalmoxiformis* (Roewer): 63, dorsal view of male; 64, lateral view of male; 65, distal portion of penis.

Figs. 66-69.—*Neocynortina dixonii*, new species: 66, lateral view of male; 67, dorsal view of male; 68, distal portion of penis; 69, distal portion of ovipositor.

Figs. 70-72.—*Pachylicus rugosus* (Banks): 70, lateral view of male; 71, lateral view of distal portion of penis; 72, dorsal view of male.

Cephalothorax smooth, eye tubercle slightly removed from the anterior margin, with a sharp forward pointing median spine. Dorsal areas clearly delineated; each area with a median row of light hair-tipped tubercles. Anal operculum with several large tubercles. Ventrally the coxae have some hair-tipped tubercles. Coxa I with a larger one near the basal area; coxa II with two larger hair-tipped tubercles at the posterior lateral border; coxa III with both anterior and posterior rows of blunt tubercles; coxa IV with numerous low hair-tipped tubercles on the anterior surface. Each free sternite with a transverse row of low hair-tipped tubercles. Spiracle slightly concealed by coxa IV.

Male penis somewhat club-shaped, distal end complex, 2 mm long.

Palpus: trochanter, 0.5 mm long; femur, 0.9; patella, 0.6; tibia, 0.8; tarsus, 0.6. Total length, 3.4 mm. Palpus armed as in figure; femur with two basal and one apical-median spine-tipped tubercles, patella with a single apical-median spine; tibia with three spine-tipped tubercles on either side; tarsus with two on either side. Palpal claw simple, smooth. Chelicerae normal in size with numerous long hairs at the distal portion of each second segment.

All segments of the legs with many investing hairs which are most numerous on the tarsi. Femora, patella, tibiae, and metatarsi of legs I-III rounded, with numerous hair-tipped tubercles. Metatarsi and tarsi more slender. Femur, tibia, and metatarsus of leg IV elongate; metatarsus with several larger spinose tubercles scattered along its length. Tarsal segments: 3-7-5-6.

Dorsal color uniform reddish-brown, dorsal areas slightly darker, venter slightly lighter. Trochanters of legs, palpi, and chelicerae much lighter, contrasting with the dorsum. Tubercles of the dorsum are lighter in some specimens. The individual opiliones often appear to be a bright reddish-brown with strongly contrasting yellow trochanters and eye tubercle spine. This coloration makes the species quite distinctive.

Female.—Total length of body, 4.1 mm; cephalothorax length, 1.3 mm; width of body at widest portion, 3 mm. Similar in appearance to male, but lacking the elongate fourth legs.

Type data.—Two males, two females, San Isidro, Puntarenas. A type specimen was not indicated by Banks. MCZ, examined.

Additional records.—Santa Maria Dota, Uricuzjo, Atenas, La Bolca (Banks' records); La Palma, one male, one female (Roewer's record) NHMS, examined; Alajuela, finca near San Roman, 13 July 1976, one male, five females, two immatures; Guanacaste, Monte-verde, 23 June 1976, two males, three females; Puntarenas, Nicoya Peninsula, fields near Cabuya, 9 July 1976, one male, two females; Puntarenas, Nicoya Peninsula, Tambor, 9 July 1976, four females, three immatures; Puntarenas, Nicoya Peninsula, reserve near Cabuya, 9 July 1976, two males, one female, two immatures.

Pachylicus cotoensis, new species

Figs. 73-76

Description of male holotype.—Total length of body, 3.1 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 2.1 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.5-0.4-0.4; Femur 1.2-1.9-1.5-1.8; Patella 0.5-0.8-0.6-0.8; Tibia 0.7-1.5-1.1-1.9; Metatarsus 1.1-1.7-1.8-2.5; Tarsus 0.5-1.1-1.1-1.2; Total 4.3-7.5-6.5-8.6.

Entire dorsum smooth, eye tubercle slightly removed from the anterior margin of the cephalothorax, prolonged into a forward pointing spine. Anterior margin of cephalothorax with a median small spine, with a slightly larger single spine lateral to the median

one on either side. Dorsal areas clearly outlined, each with a median row of low spinose tubercles, median ones larger. Free tergites similarly armed. Tergite III with a single median and two lateral spines; anal operculum with some tubercles. Ventrally, coxal surfaces only roughened; posterior border of coxa III with larger tooth-like tubercles, a larger blunt spine on the posterior lateral border of coxa IV. This spine obscures the spiracles. Free tergites relatively smooth.

Penis a chitinous shaft, 1.5 mm long.

Palpus: trochanter 0.3 mm long; femur, 0.6; patella, 0.3; tibia, 0.5; and tarsus, 0.5. Total length, 2.2 mm. Palpus with a smooth surface; tibia and tarsus enlarged, almost bulbous. Tarsus with an unusual fleshy protuberance at the proximal median surface. Femur and patella each with an apical-median spine.

All segments of the legs with hairs and a roughened appearance. Trochanters with various spines and tubercles as illustrated. Femur, patella, and tibia of leg I somewhat enlarged. Tarsal segments: 3-9-5-6.

Dorsum reddish-brown in color. Palpi, chelicerae, and trochanters and tarsi of legs much lighter. Tip of spine of eye tubercle also lighter.

Female.—Total length of body, 3.5 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 2 mm. Length of femora: 1.1 mm-1.7 mm-1.3 mm-1.6 mm. Similar in appearance to the male, but lacking the fleshy protuberance of the palpal tarsus and the enlarged segments of leg I.

Type data.—Male holotype, male paratype, and three female paratypes from Coto, Puntarenas, 30 August 1957 (E. Dixon).

Remarks.—This species differs from the other members of this genus chiefly by its possession of the unusual fleshy protuberance on the palpal tarsus.

Pachylicus foveolatus, new species

Figs. 77-80

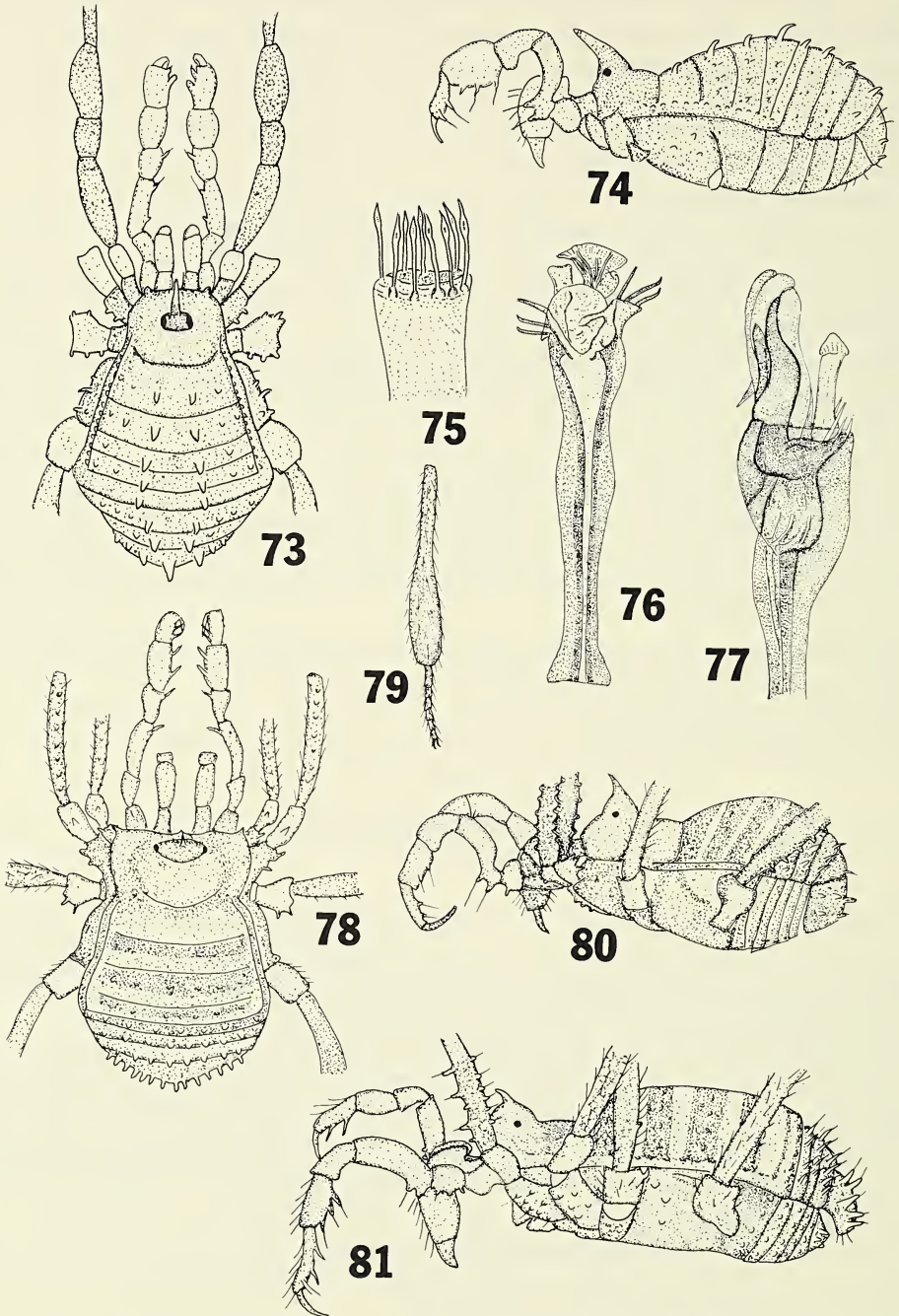
Description of male holotype.—Total length of body, 3 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 2.2 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.4-0.3-0.5; Femur 0.9-1.5-1.2-2.2; Patella 0.5-0.7-0.4-0.9; Tibia 0.7-1.3-0.9-1.9; Metatarsus 1.1-1.6-1.3-2.5; Tarsus 0.7-0.9-0.8-0.9; Total 4.2-6.4-4.9-8.9.

Dorsum, including cephalothorax smooth; eye tubercle slightly removed from the anterior margin of the cephalothorax, terminating in a sharp dorsal spine. Dorsal areas clearly defined by darker markings. Each dorsal area with a transverse row of low tubercles which are somewhat larger on the fifth area. Each free tergite with a transverse row of low spines which are somewhat more conspicuous on tergite III. Coxae, genital operculum, and free sternites smooth. Coxa II with a small spine on the posterior distal portion, a few low tubercles on the posterior margin of coxa II. Coxa IV with some spinose hairs, spiracle partially concealed by coxa IV. Free sternites smooth, dorsal portion of anal operculum with a few low spines.

Penis 0.96 mm long, a slender, sclerotized shaft.

Palpus: trochanter, 0.4 mm long; femur, 0.5; patella, 0.4; tibia, 0.5; and tarsus, 0.3. Total length, 2.1 mm. Palpus armed as in figure; femur with a median apical spine. Chelicera not enlarged.

Trochanters of legs smooth, with a few low spines on the posterior border of trochanter III. Femora, patellae, and tibiae rounded; metatarsi slender; all segments with



Figs. 73-76.—*Pachylicus cotoensis*, new species: 73, dorsal view of male; 74, lateral view of male; 75, distal portion of ovipositor; 76, dorsal view of penis.

Figs. 77-80.—*Pachylicus foveolatus* new species: 77, lateral view of distal portion of penis; 78, dorsal view of male; 79, metatarsus and tarsus of leg IV of male; 80, lateral view of male.

Fig. 81.—*Pachylicus hirsuta* Roewer: 81, lateral view of male.

numerous hairs. Femora of legs I, II, and IV with larger spinous tubercles; distal portion of metatarsus IV enlarged. Tarsal segments: 3-7-5-6.

Dorsum, femora, patellae, tibiae, and metatarsi of legs reddish-brown; venter, trochanters, and tarsi of legs as well as chelicerae and palpi lighter. Trochanters contrasting strongly with the dorsum in color. Distal portion of tibiae and proximal portion of metatarsi somewhat lighter.

Female.—Total length of body, 2.7 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.7 mm. Similar in appearance to male, but lacking the enlargement of metatarsus IV.

Type data.—Male holotype, two female paratypes, and three immatures from Manuel Antonio National Park, Puntarenas, 19 and 21 June 1976. These animals were found among the dead and decaying leaves on the ground.

Remarks.—*Pachylicus foveolatus* differs from the other species of this genus in its secondary sexual characters and the form of the eye tubercle.

Pachylicus hirsutus (Roewer), new combination

Figs. 82-84

Brimma hirsutus Roewer 1949a:19, figs. 16a-f.

Description of male.—Total length of body, 2.4 mm; cephalothorax length, 0.85; width of body at widest portion, 1.75 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.3-0.3-0.4; Femur 0.7-1.1-1.0-3.0; Patella 0.4-0.5-0.4-1.1; Tibia 0.6-1.0-0.8-3.2; Metatarsus 0.8-1.1-1.1-2.6; Tarsus 0.6-1.0-0.7-0.9; Total 3.3-5.0-4.3-11.2.

Cephalothorax somewhat narrow, abdomen wider. Dorsum smooth, the legs with spinose hairs which give the animal a somewhat hirsute appearance. Eye tubercles dorsally with a forward pointing spine, eyes at base. Each free tergite with a transverse row of hair-tipped low spines. Dorsal portion of anal operculum with numerous small hair-tipped spines. Ventral surfaces of coxae and genital operculum quite smooth. Coxa II with small spines at the distal posterior portion; coxa III with a posterior row of low tubercles. Spiracles partially concealed by a short dorsal spine from trochanter IV. Free sternites smooth, ventral portion of anal operculum with spines.

Penis 0.9 mm long, complex in appearance.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.2; tibia, 0.4; tarsus, 0.2. Total length, 1.4 mm. Palpus armed as in figure. Basal segment of chelicera with a slight dorsal enlargement.

All segments of legs, including the coxae, with spinose hairs. Tarsal segments: 3-6-5-5. Femora, patellae, and tibiae of legs I-III slightly enlarged. Femur of leg I with spinose tubercles arranged as in figure. Femur IV elongate, with a low spine at the apical portion. Metatarsus IV somewhat curved with a small apical spine.

Color of entire animal light yellow brown, dorsal areas of abdomen with darker central areas. Trochanter of legs somewhat lighter, remainder legs concolorous with the dorsum. Cephalothorax with black pencillings, palpi likewise netted with darker pencillings.

Female.—Total length of body, 2.5 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.8 mm. Length of femora: 0.65 mm-0.9 mm-0.9 mm-1.05 mm. Similar in general appearance to the male. The chief difference is to be noted in the length of the femora. Femur IV, particularly, is much shorter. The femora, patellae, and tibiae are somewhat more spinose in appearance than those of the male.

Type data.—Male holotype from Waldeck Farm, 45 km northwest of Limon, Limon (Roewer's record), NHMS, examined.

Additional records.—Puntarenas, Coto, 27 October 1957 (E. Dixon), one male, two females, eight immatures; Puntarenas, Golfito, 20 October 1957 (E. Dixon), one male, one female, one immature; Puntarenas, Agua Buena, 27 October 1957 (E. Dixon) one male; Puntarenas, Corredor, 20 October 1957 (E. Dixon) one male; Puntarenas, Las Cruces near San Vito, 1 August 1975, one male, one female; Puntarenas, Llorona, Osa Peninsula, 9 August, 1978, one male.

Remarks.—While most of the male specimens examined exhibited the usual elongate fourth leg, the male from Agua Buena had a much shorter fourth leg, with the femur being only 1.5 mm long.

Pachylicus hispidus, new species

Figs. 85-87

Description of male holotype.—Total length of body, 2.8 mm; cephalothorax length, 0.8 mm; width of body at widest point, 1.6 mm cephalothorax length, 0.8 mm; width of body at widest point, 1.6 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.4-0.4-0.4; Femur 1.3-1.9-1.4-1.8; Patella 0.4-0.6-0.5-0.7; Tibia 0.8-1.7-1.1-0.9; Metatarsus 1.6-1.9-1.5-2.1; Tarsus 0.5-2.1-1.0-1.4; Total 4.9-8.6-5.9-7.3.

Cephalothorax smooth, eye tubercle slightly removed from anterior margin, with a short spine projecting upward. Eyes large at base. Anterior margin of cephalothorax with a small projection in center and one on each side just laterad to the chelicerae. Dorsal areas not clearly defined, each with a transverse irregularly placed row of low hair-bearing tubercles. Free tergites with similar rows of tubercles, a few scattered ones on the anal operculum. Venter with all portions having hair-bearing low tubercles. Coxa II with a few larger tubercles at the anterior portion, similar tubercles on the posterior margin. Coxa IV with some large hair-bearing tubercles on the dorsal area, those of the ventral portion smaller. Each free sternite with a transverse row of hair-bearing low tubercles; anal operculum with numerous hair-bearing tubercles. Spiracle partially concealed by coxa IV.

Penis 1.2 mm long, with a distinctive configuration as illustrated.

Palpus: trochanter, 0.2 mm long; femur, 0.7; patella, 0.5; tibia, 0.5; tarsus, 0.6. Total length, 2.5 mm. Palpal segments quite smooth with ventral spines. Femur and patella each with an apical median spine. Chelicerae small, second segment of each with several hair-bearing tubercles.

All segments of the legs but the tarsi roughly tuberculate, clothed with many hairs. Tarsal segments: 3-7-5-6.

Color of dorsum and venter a uniform yellow brown; palpi and chelicerae and trochanters of legs somewhat lighter than the dorsum.

Female.—Total length of body, 2.8 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.6 mm. Nearly identical in appearance with male, no apparent sexual dimorphism present. Ovipositor as illustrated.

Type data.—Male holotype and female paratype from interior of La Cueva de Damas, near Manuel Antonio National Park, Puntarenas 22 June 1976.

Remarks.—The most distinctive feature of this species is the general spinose appearance. Although they were collected from within a cave, they showed no special adaptations for cave life.

Pachylicus spinatus, new species

Figs. 88-92

Description of male holotype.—Total length of body, 2.5 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.9 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.1-0.4-0.4-0.4; Femur 0.9-1.7-1.2-3.1; Patella 0.4-0.7-0.4-0.8; Tibia 0.8-1.4-1.1-2.7; Metatarsus 1.1-1.7-1.5-3.5; Tarsus 0.8-1.2-0.8-0.8; Total 4.1-7.1-5.4-11.3.

Cephalothorax narrow, with a small spine on each side of the anterior margin. Eye tubercle removed from the anterior margin, with a forward pointing median spine and with two small spines behind the eye tubercle. Five dorsal areas distinct; all areas and free tergites armed as in figure. These spines are tipped with spinose hairs; the spines are somewhat larger on the free tergites than on the dorsal areas. Venter somewhat granulate, but with only a few conspicuous tubercles. A few of these are located on the posterior border of coxa III and a single large one is on the posterior portion of coxa IV. Anal operculum with blunt spines similar to those of the free tergites. Spiracle hidden.

Penis with a very complex structure, as in figure.

Palpus: trochanter, 0.2 mm long; femur, 0.4; patella, 0.3; tibia, 0.4; and tarsus, 0.2. Total length, 1.5 mm. Palpus armed as in figure; both femur and patella with anterior median spines; tibia slightly enlarged ventrally. Chelicerae small, with some hairs.

Trochanter and coxae of legs with some spines; femora of legs I, II, and IV with larger spines which are somewhat larger at the distal portion of femur IV. Femora, patellae, and tibiae rounded, larger in diameter than the metatarsi and tarsi. All segments with numerous hairs. Tarsal segments: 3-6-5-5.

Color of body uniform brown. Palpi and trochanters of legs somewhat lighter; distal portion of metatarsi and tarsi of palpus lighter. Spines of dorsum also light brown in color.

Female.—Total length of body 2.9 mm; cephalothorax, 0.8 mm; width of body at widest portion, 2.1 mm. Similar in appearance to male, but with the femur and tibia of leg IV much shorter, with the femur being 1.7 mm long and the tibia 1.5 mm. Ovipositor with a blunt double anterior portion and with several large spines as illustrated.

Type data.—Male holotype, male paratype, and two female paratypes from Llorona, Osa Peninsula, Puntarenas, 9 August 1978.

Additional record.—Puntarenas, Osa Peninsula, Swamp trail, Llorona, 23 August 1979, one male.

Remarks.—This species is related to *Pachylicus rugosus* but the appearance of the eye tubercle, the numbers of the tarsal segments, and the structure of the male penis all clearly differentiate it.

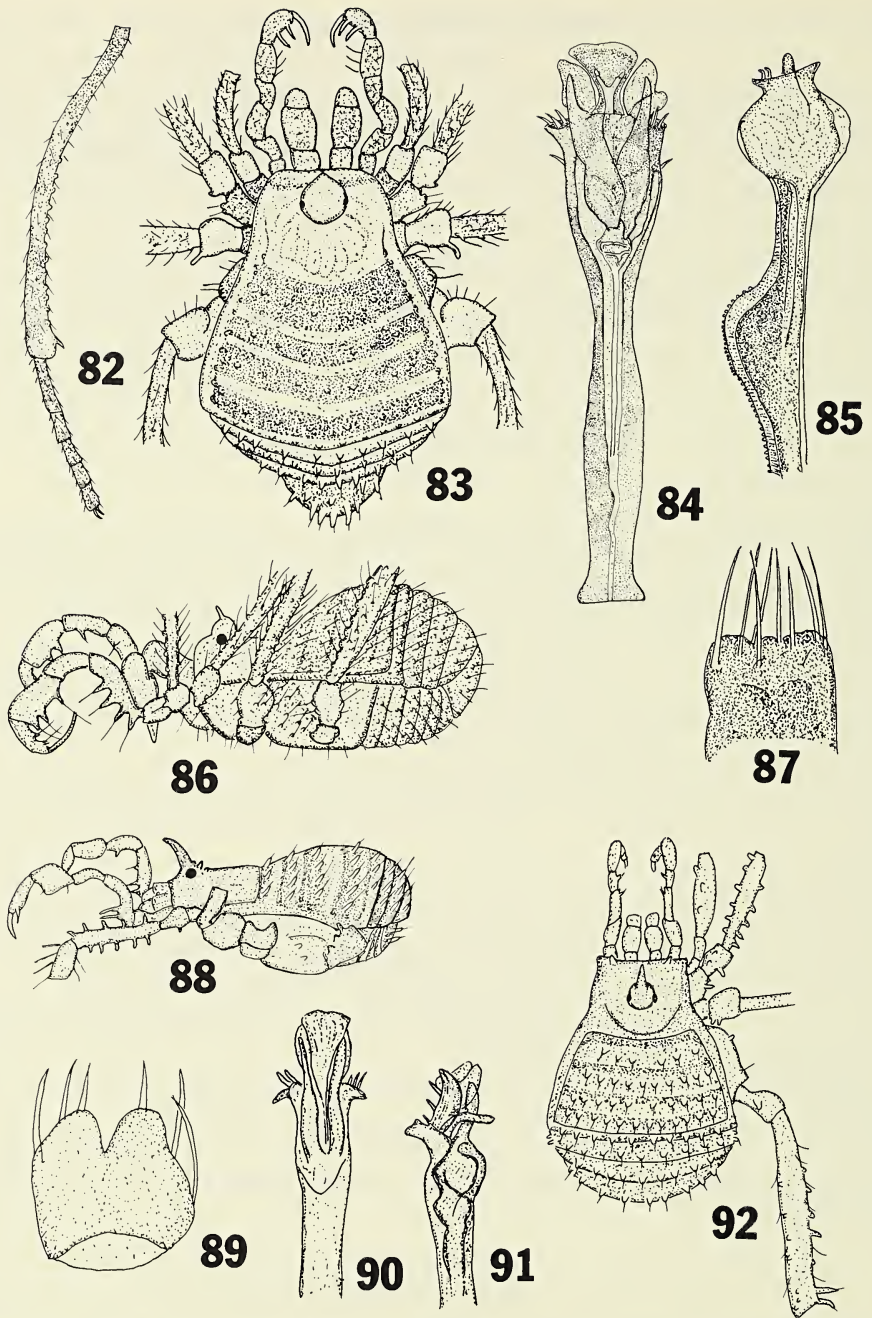
Panopiliops Roewer

Panoplia Roewer 1949a:42 (nec *Panoplia* Huebner 1925).

Panopiliops Roewer 1949c:144 (replacement name).

Type species.—*Panopiliops reimoseri* (Roewer).

Diagnosis.—Medium sized phalangodids with the eye tubercle slightly removed from the anterior margin of the cephalothorax, rounded, and with a single dorsal spine. Dorsum with five areas, the borders of which are parallel; first area without a median line. Tarsal segments 4-more than 6-5-5 or 6. Metatarsi without astraguli or calcanei. Tarsal



Figs. 82-84.—*Pachylicus hirsuta* Roewer: 82, tibia and tarsus of leg IV of male; 83, dorsal view of male; 84, ventral view of penis.

Figs. 85-87.—*Pachylicus hispidus*, new species: 85, lateral view of distal portion of penis; 86, lateral view of male; 87, distal portion of ovipositor.

Figs. 88-92.—*Pachylicus spinatus*, new species: 88, lateral view of male; 89, distal portion of ovipositor; 90, dorsal view of distal portion of penis; 91, lateral view of distal portion of penis; 92, dorsal view of male.

claws of tarsi III and IV double, smooth, arising independently. Distitarsi of legs I and II, 2 and 3 respectively.

Remarks.—At present there are but two species in this genus.

Panopiliops reimoseri (Roewer)

Figs. 93-96

Panoplia reimoseri Roewer 1949a:42, figs. 74a-e.

Panopiliops reimoseri Roewer 1949c:144.

Description of male.—Total length of body, 2.8 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 1.9 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.3-0.4-0.4-0.6; Femur 1.4-2.6-2.2-5.5; Patella 0.5-0.6-0.6-1.0; Tibia 1.1-2.0-1.6-4.9; Metatarsus 1.5-2.8-2.5-5.8; Tarsus 0.6-1.9-1.1-1.4; Total 5.4-10.3-8.4-19.2.

Cephalothorax smooth, eye tubercle slightly removed from the anterior margin, with a dorsal sharp spine; anterior margin of cephalothorax smooth. Abdominal surface smooth except for a few low tubercles on the lateral margins and paired spines on the median portion of the dorsal areas. These are small on the first area and become progressively larger on the posterior areas with those of the fourth area being the largest; those of the fifth area are somewhat smaller. A few smaller tubercles also present laterad to the median spines of the fifth area. First free tergite with a horizontal row of low tubercles, with the central ones somewhat larger. Spines of the second and third free tergites much larger; several large spines present on the anal operculum. Venter slightly granulate, coxa I with a few larger hair-tipped tubercles on the anterior border. Coxa III with a few teeth on the anterior and posterior borders. Coxa IV with several low spine-tipped tubercles. Each free sternite with a transverse row of every low tubercles. Spiracle partially concealed.

Penis as illustrated.

Palpus: trochanter, 0.1 mm; femur, 0.5; patella, 0.4; tibia, 0.4; tarsus, 0.4. Total length, 1.8 mm. Palpus armed as in figure. Femur and patella each with an apical median spine. Chelicera not enlarged.

All segments of legs smooth. Femur I with somewhat enlarged tubercles. Tarsal segments: 4-7-5-6.

Color of entire body light reddish-brown, trochanters of legs lighter.

Female.—Total length of body, 2.8 mm; cephalothorax length, 0.8 mm; width at widest portion, 2.2 mm. Similar in appearance to male but with shorter legs. Femora: 1.1 mm-1.8 mm-1.5 mm-2.5 mm. Total length of legs: 4.3 mm-7.5 mm-6.1 mm-9.6 mm.

Type data.—Male holotype and female paratypes from Hamburg Farm, 20 km north of Siquirres, Limon (Roewer's record), NHMS, female paratype examined.

Additional records.—Cartago, Turrialba, 22 July 1976, three males, three females; Heredia, Finca La Selva, 25 September 1979 one male.

Panopiliops inops, new species

Figs. 97-100

Description of female holotype.—Total length of body, 2.9 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 1.8 mm. Length of legs (I-II-III-IV in mm):

Trochanter 0.3-0.4-0.4-0.4; Femur 1.1-1.6-1.1-1.6; Patella 0.4-0.7-0.5-0.6; Tibia 0.8-1.3-0.9-1.4; Metatarsus 1.0-1.4-1.1-1.5; Tarsus 0.7-1.6-1.0-1.0; Total 4.3-7.0-5.0-6.5.

Entire body surface, including all segments of legs but the tarsi with numerous low granulations. Eye tubercle on the anterior margin of the cephalothorax, without eyes, with a sharply pointed spine at the apex and with numerous larger tubercles present at the base of the spine. Dorsal areas not clearly indicated. Free tergites and anal operculum with numerous low granulations which are somewhat larger on the third free tergite and the anal operculum. All ventral surfaces with granulations less abundant on the genital operculum and largest on coxa IV. Spiracle concealed by low spines from coxa IV.

Ovipositor as illustrated.

Palpus: trochanter, 0.3 mm long; femur, 1.0; patella, 0.4; tibia, 0.7; and tarsus 0.5. Total length, 2.9 mm. Palpus with spines as illustrated. Femur and patella each with an apical-median spine. Proximal segment of chelicera with small dorsal elevation. Both chelicera and palpus somewhat smoother than remaining portions of the body.

Legs slender, all segments but the tarsi with low granulations, some larger ones present on the trochanters. Many hairs present on all segments. Tarsal segments: 4-7-5-5. Femur IV slightly curved, first tarsal segment of leg III elongate.

Entire animal very light yellow, appendages somewhat lighter.

Type data.—Female holotype from Coto, Puntarenas, 7 May 1957 (E. Dixon).

Remarks.—Though the label does not indicate that this specimen was collected in a cave, it has the typical appearance of cave adapted species including the lack of eyes, the pale coloration, and the slightly elongated appendages.

It differs from *P. reimoseri* in its general appearance, particularly in its possession of cave-adapted features.

Phalangoduna Roewer

Phalangoduna Roewer 1949a:33.

Sempalus Roewer 1949a:41. **NEW SYNONYMY.**

Type species.—*Phalangoduna granosa* Roewer.

Diagnosis.—Phalangodids of medium size, eye tubercle located on anterior margin of cephalothorax. Dorsum with five areas, first without median line, borders parallel. Spiracles partially concealed by portions of coxae IV. Tarsal segments: 4-6-5-5. Distitarsus of first tarsus with two segments, second with three. Metatarsi without astraguli or calcanei; tarsal claws of legs III and IV, arising independently, double, untoothed.

Phalangoduna granosa Roewer

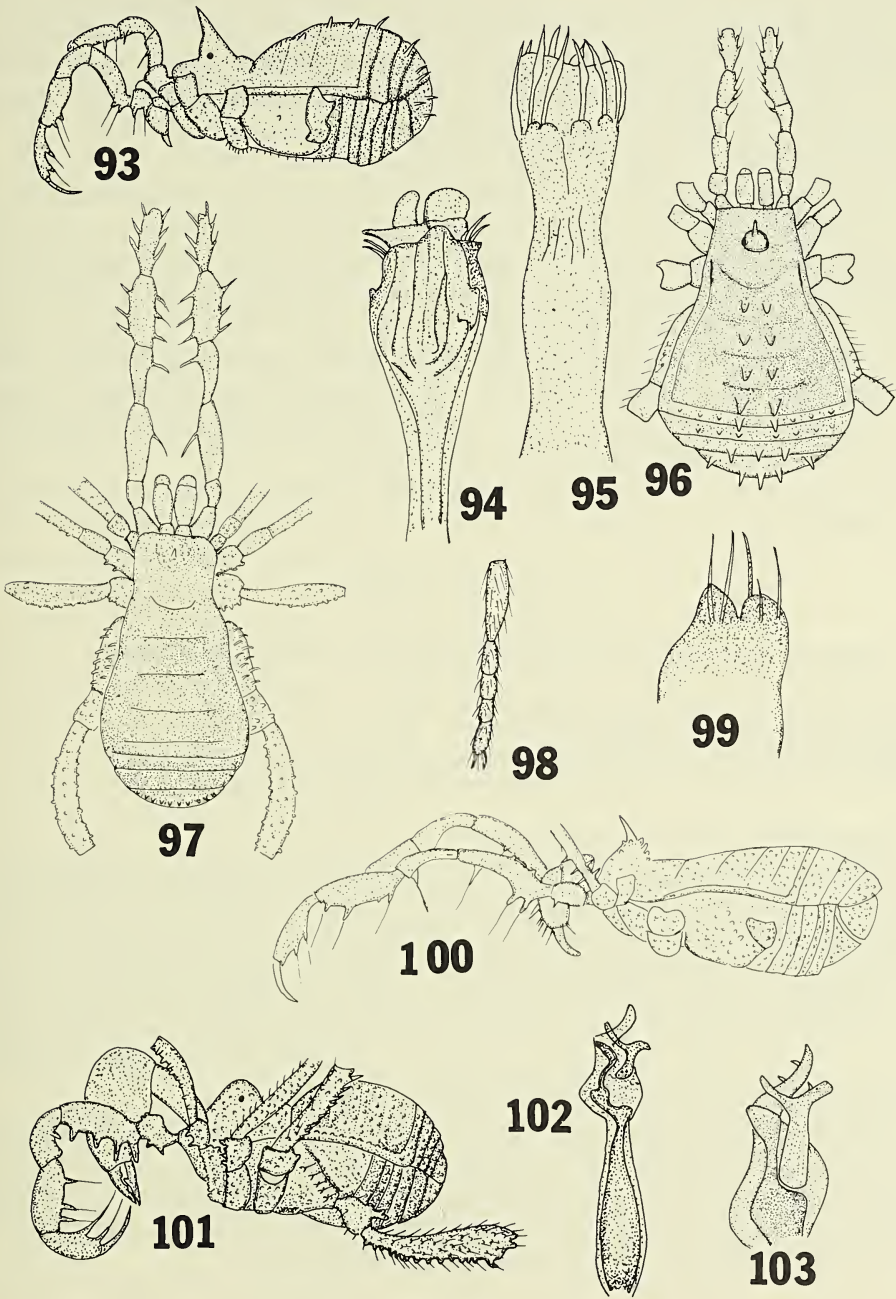
Figs. 101-103

Phalangoduna granosa Roewer 1949a:33, figs. 52a-e.

Sempalus setulosus Roewer 1949a:41, figs. 70a-e. **NEW SYNONYMY.**

Description of male holotype.—Total length of body, 2.6 mm; cephalothorax length, 0.75 mm; width of body at widest portion, 1.8 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.3-0.4-0.4; Femur 0.8-2.2-1.2-1.6; Patella 0.4-0.6-0.5-0.7; Tibia 0.7-1.3-1.0-1.4; Metatarsus 1.1-1.5-1.5-1.9; Tarsus 0.6-0.9-0.7-1.0; Total 3.8-6.8-5.3-7.0.

A relatively small animal, entire surface of dorsum very granulate; eye tubercle located on anterior margin of the cephalothorax, rounded above, with numerous granulations.



Figs. 93-96.—*Panopiliops reimoseri* (Roewer): 93, lateral view of male; 94, dorsal view of tip of penis; 95, tip of ovipositor; 96, dorsal view of male.

Figs. 97-100.—*Panopiliops inops*, new species: 97, dorsal view of female; 98, tarsus of leg III of female; 99, distal portion of ovipositor; 100, lateral view of female.

Figs. 101-103.—*Phalangoduna granosa* Roewer: 101, lateral view of male; 102, distal portion of penis; 103, distal portion of penis enlarged.

Anterior margin of cephalothorax with three small tubercles at the lateral margin. Abdomen arched slightly, areas visible, all dorsal areas with numerous granulations. Free tergites likewise with granulations. All ventral areas granulate, coxa II with a posterior row of slightly enlarged tubercles; coxa III with anterior and posterior rows of tooth-like granulations. Coxa IV with conspicuous granulations.

Penis a somewhat rounded shaft, 1.08 mm long.

Palpus: trochanter, 0.3 mm long; femur, 0.9; patella, 0.4; tibia, 0.7; nd tarsus, 0.7. Total length, 3 mm. Palpus armed as in figure.

Legs with numerous granulations, trochanters with heavier hair-tipped granulations which are also present on the femora, patellae, and tibiae. Metatarsi and tarsi clothed with numerous hairs. Tarsal segments: 4-6-5-5.

Entire dorsum and appendages light yellow brown; tarsi of legs somewhat lighter.

Type data.—Male holotype from La Palma (Roewer's record), NHMS, examined.

Additional record.—Darien, Panama (Roewer's record), NHMS, not examined. This record is of the female holotype of *Sempalus setulosus*.

Remarks.—A close study of the descriptions of these two species convinces us that they are identical.

Stygnoleptes Banks

Stygnoleptes Banks 1914:682; Roewer 1939:160; Goodnight and Goodnight, 1947b:2.

Chersobleptes Soerensen 1932:271. **NEW SYNONYMY.**

Mochlus Roewer 1933:280 (Nec *Mochlus* Gunther 1864). **NEW SYNONYMY.**

Piercenia Roewer 1934:304. **NEW SYNONYMY.**

Cippanus Roewer 1933:278. Goodnight and Goodnight 1942c:1. **NEW SYNONYMY.**

Cynortina Goodnight and Goodnight, 1953:14 (in part). **NEW SYNONYMY.**

Type species.—*Stygnoleptes analis* Banks.

Diagnosis.—Small animals having a low eye tubercle which is slightly removed from the anterior margin of the cephalothorax. Dorsum with five areas, first without a median line, margins of areas parallel. Tarsal segments variable in number: 3-6-4-5; 3-6-5-5; or 3-5-4-5. Distitarsus of first tarsus with two segments, second with three. Tarsi of third and fourth legs without scopulae, double claws smooth, arising individually. Metatarsi not divided into astraguli or calcanei. Male penis is a sclerotized shaft. Secondary sexual characteristics consisting chiefly of increased spination of legs, presence of a spine on the anal operculum, and enlarged basal segments of the tarsi of the males.

Remarks.—This genus is closely related to *Parascotolemon* Roewer, differing chiefly in the number of tarsal segments and general appearance. Though described in 1913 by Banks, this genus has been described several times under other names by other workers; possibly this is due to the lack of recognition by other workers of the considerable variation that exists among the individuals of the single species.

Stygnoleptes analis Banks

Figs. 108-110

Stygnoleptes analis Banks 1914:682 pl. 28, figs. 6, 13; Roewer 1931:160, fig. 25; Goodnight and Goodnight 1947b:3, figs. 7-10.

Chersobleptes boveli Soerensen 1932:271-272. **NEW SYNONYMY.**

Mochlus ventralis Roewer 1933:280, fig. 4. **NEW SYNONYMY.**

Cippanus calcartibialis Roewer 1933:278, fig. 2. **NEW SYNONYMY.**

Cippanus adornus Goodnight and Goodnight 1942c:1, figs. 5-9. **NEW SYNONYMY.**

Description of male.—Total length of body, 2.6 mm; cephalothorax length, 0.7 mm; width of body at widest portion, 1.2 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.2-0.2-0.3; Femur 0.5-0.8-0.8-1.0; Patella 0.3-0.4-0.2-0.4; Tibia 0.4-0.8-0.5-0.8; Metatarsus 0.5-0.9-0.8-1.2; Tarsus 0.4-0.8-0.5-0.8; Total 2.3-3.9-3.0-4.5.

A small animal, cephalothorax somewhat narrower than the abdomen, body arched. Eye tubercle low, rounded. Dorsal areas poorly defined. Both cephalothorax and abdomen with only a few granulations on the lateral borders. Free tergites smooth, a small spine present on either side of the third and sometimes on the second. Ventral surfaces likewise smooth. Coxa III with a few anterior and posterior low tubercles; IV with some low tubercles on the anterior surface. Anal operculum usually with a large median spine. Spiracles partially concealed by low tubercles of the first free sternite.

Penis 0.8 mm long, with soft portions extending from the sclerotized portions.

Palpus: trochanter 0.2 mm long; femur, 0.3; patella, 0.2; tibia, 0.3; and tarsus, 0.2. Total length, 1.2 mm. Chelicera not enlarged.

All segments of legs with investing hairs. First segment of tarsus III enlarged; femur III with some spinose tubercles; tibia IV with spines as illustrated.

Entire dorsum deep reddish-brown; chelicera and palpus very light yellow. Legs marked as follows: leg I, trochanter and femur (except for distal portion) and distal tarsal segments light, remainder of leg darker; leg II similar to I but with tarsal segments 1 and 6 dark, others light; leg III similar to leg II with tarsal segment II darker; leg IV with the trochanter and femur light above and dark below, patella and tibia dark, spines of tibia light, metatarsus and tarsus dark.

Female.—Total length of body, 2.2 mm; cephalothorax length, 0.7 mm; width of body at widest portion, 1.6 mm. Similar in appearance to male but lacking the enlarged spine of the anal operculum and the enlarged basal segments of tarsus III. Ovipositor with a bilobed tip and a few bristle-like spines.

Type data.—Male holotype from Turrialba, Cartago (Banks' record), MCZ, examined.

Additional records.—Limon, Hamburg Farm 20 km N of Siquirres, five males, two females (Roewer's records of *Cippanus calcartibialis* and *Mochlus ventralis*); Costa Rica, one male (Soerensen's record for *Chersobleptes boveli*), NRS, examined; Guanacaste, Monteverde, Sendero Brillante, 10 July 1978, one male; Panama, Barro Colorado Island 4 August 1938 (E. C. Williams, Jr.), AMNH, examined, one male, one female (*Cippanus adornus* Goodnight and Goodnight).

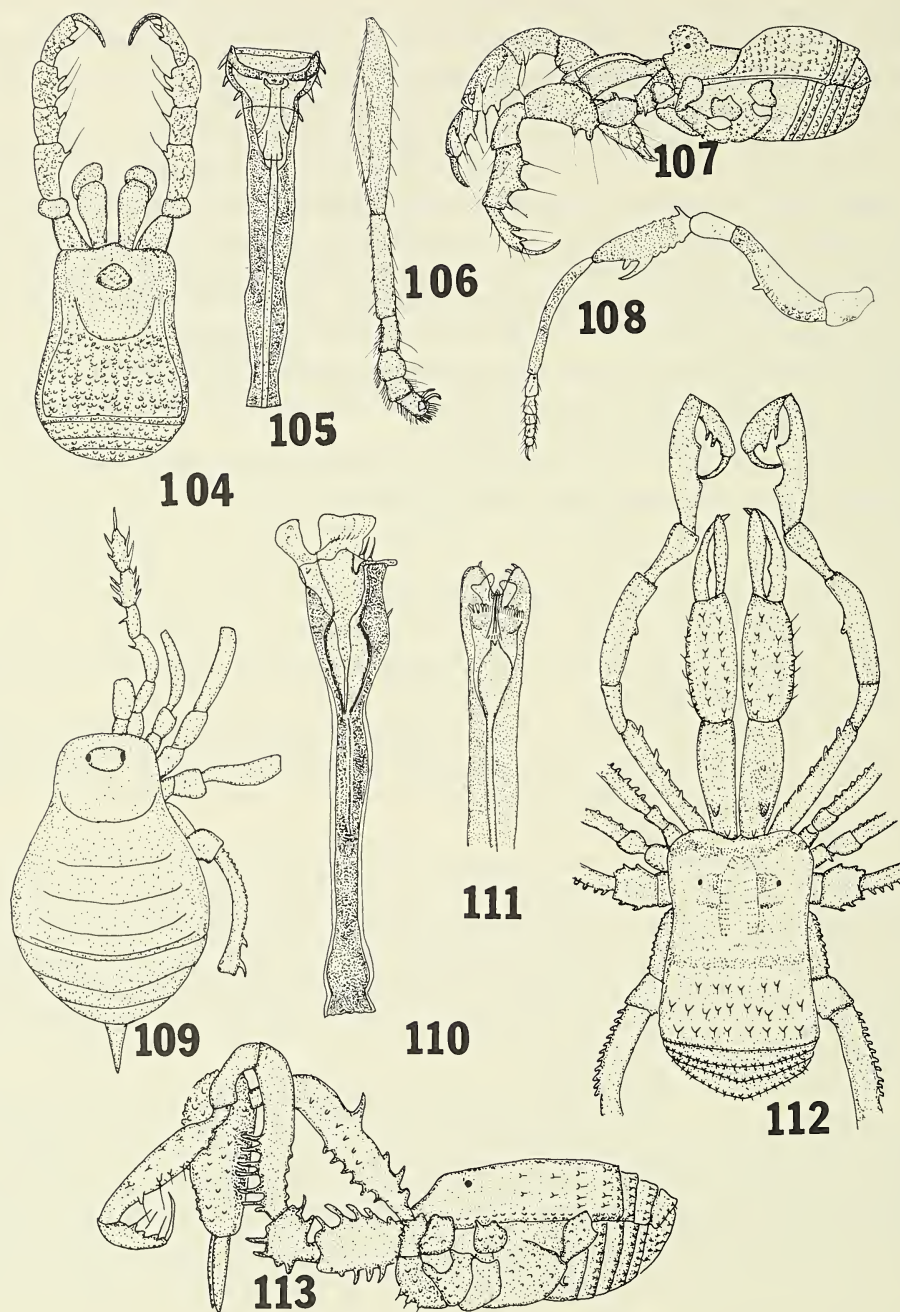
Remarks.—A study of the various specimens has demonstrated that there is considerable variation in the number of tarsal segments as well as the nature of the secondary sexual characteristics of the males. This has, in part, lead to the numerous descriptions. While the spination of tibia IV remains quite constant, the enlargement of tarsal segments appears to vary. Roewer noted that the male specimen which he studied from Hamburg farm (*C. calcartibialis*) had the basal segments of tarsi II and III enlarged. Likewise there is considerable variation in the size of the spine of the anal operculum. In some it is very large and conspicuous, in others, it is much less enlarged. Also the small spines of the free tergites may vary in size and number. The tarsal segments also vary as noted above.

Stygnomma Roewer

Phalangodes Packard 1888:52 (in part).

Scotolemon Banks 1901:671 (in part).

Neoscootolemon Roewer 1912:149 (in part); 1923:112 (in part).



Figs. 104-107.—*Pellobunus insularis* Banks: 104, dorsal view of male; 105, dorsal view of penis; 106, metatarsus and tarsus of leg III of male; 107, lateral view of male.

Figs. 108-110.—*Stygnoleptes analis* Banks: 108, lateral view of leg IV of male; 109, dorsal view of male; 110, lateral view of penis.

Figs. 111-113.—*Stygnomma fuhrmanni* Roewer: 111, ventral view of penis; 112, dorsal view of male; 113, lateral view of male.

Stygnomma Roewer 1914:155; 1923:244; 1949b:256; Petrunkevitch 1925:62; Goodnight and Goodnight 1951:3.

Zygobunus Chamberlin 1925:245; Roewer 1927:545; 1949b:256; Goodnight and Goodnight 1942c:4.

Stygnommatiplus Roewer 1927:543.

Poascola Roewer 1933:281, 1949b:256.

Antagona Goodnight and Goodnight 1942a:6.

Citrinus Goodnight and Goodnight 1942a:4.

Rula Goodnight and Goodnight 1942b:13; 1945:62.

Flaccus Goodnight and Goodnight 1947a:9.

Type species.—*Stygnomma fuhrmanni* Roewer.

Diagnosis.—Medium to large animals without a common eye tubercle, with five dorsal areas; first area without a median line, borders parallel. Tarsal segments somewhat variable in number, all usually numbering more than six, though the first may vary from four to eight. Distitarsus of tarsus I with two segments; tarsus II with three. Tarsi of legs III and IV without scopulae and with simple untoothed claws which arise independently. Femur of leg I normal in size; metatarsus of leg III not divided into astraguli or calcanei. Palpus and chelicera of male often enlarged, degree of enlargement varying with the individual specimen. Secondary characteristics of the male usually consisting of increased size and spination of the palpus and usually some enlargement of a portion of metatarsus III.

Remarks.—Species within this genus are separated on the basis of size, general body configuration, secondary sexual characters, and spination. Though the members of this genus are widespread in their distribution, they are not commonly found. *S. fuhrmanni* is the southernmost representative of the genus and is easily recognized when found. Because of its unusual appearance, it does attract attention and possibly this accounts for its being described so many times.

In our paper (1951) we concluded that members of this genus should be included in the subfamily Phalangodidae. Roewer and other authors had considered them to be in a separate subfamily based on their lack of an eye tubercle. We felt, at that time, that this was too variable a trait to be used for separation of subfamilies; for we had specimens which showed a condition intermediate between having and not having an eye tubercle.

Stygnomma fuhrmanni Roewer

Figs. 111-113

Stygnomma fuhrmanni Roewer 1914:155, pl. 8, fig. 7, 1923:245; Goodnight and Goodnight, 1951:4, figs. 1-3.

Stygnomma rufum Petrunkevitch 1925:62.

Stygnomma armatum Petrunkevitch 1925:63, fig. 1.

Zygobunus barronus Chamberlin 1925:245; Roewer 1927:546; Goodnight and Goodnight 1942c:4, figs. 10-12.

Stygnommatiplus rufus Roewer 1927:546.

Stygnommatiplus armatum Roewer 1927:544, fig. 6.

Poascola reimoseri Roewer 1933:281, fig. 5.

Description of male.—Total length of body, 4 mm; width of body at widest point, 2.6 mm; cephalothorax length, 1.8 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.8-1.1-0.9-1.1; Femur 3.4-4.2-4.1-4.8; Patella 1.1-1.3-1.5-1.4; Tibia 3.2-3.2-4.6-3.9; Metatarsus 4.8-6.5-4.1-5.8; Tarsus 2.7-5.5-2.7-3.4; Total 16.0-21.8-17.9-20.4.

A large animal, dorsum covered with low hair-tipped tubercles which are less conspicuous on the cephalothorax and are arranged in rows on the dorsal areas and along the sides of the dorsum, free sternites, and tergites. Eyes widely separated, placed directly on the cephalothorax, well removed from the anterior margin and with a very low elevation between them. Five dorsal areas indicated by transverse rows of low tubercles, but not clearly defined. First area without a median line. Each free tergite with a transverse row of low tubercles which are hair-tipped; both portions of anal operculum heavily covered with similar tubercles. Venter with coxae of palpi greatly enlarged, curving forward, spined. Coxa I with a ventral row of three to four large tubercles as well as several low ones; coxa II with numerous tubercles; III with similar tubercles as well as a posterior row of blunt teeth; IV with numerous hair-tipped tubercles, some slightly enlarged. Genital operculum similarly tuberculate; spiracles clearly visible. Free sternites each with a transverse row of hair-tipped tubercles.

Penis a sclerotized shaft, 2.3 mm long.

Palpus: trochanter, 1.1 mm long; femur 4.1; patella, 1.8; tibia, 3.7; and tarsus, 1.5. Total length, 12.2 mm. Retrolateral surface of palpus as in figure; prolateral surface with femur having low tubercles in the median area, tibia with low spines, one approximately in the center, the others at the distal third. Chelicerae greatly enlarged. Ventral surface with numerous spinose projections, distal segments with numerous hair-tipped tubercles.

Trochanter of legs with hair-tipped tubercles, all femora with rows of slightly enlarged tubercles. Femora III and IV slightly heavier than I and II. Tarsal segments: 8-14-6-7.

Color of dorsum venter and most segments of the appendages a uniform reddish-brown. Coxae of legs somewhat lighter, distal portions of tibiae and tarsi lighter.

Female.—Total length of body, 4.9 mm; cephalothorax length, 1.6 mm; width of body at widest portion, 3.3 mm. Similar in appearance to male, but palpus and chelicera not so strongly developed. Palpus only 7.6 mm long. Chelicera and legs likewise shorter. Ovipositor with rounded tip surrounded by 10 heavy spines.

Type data.—Plateau of Camelia, Colombia (Roewer's data) (apparently a male, place of disposition of type was not available to us).

Additional records.—Alajuela, Volcan Poas (Roewer's record for *Poascola reimoseri*); Panama, Barro Colorado Island (*Zygobunus barronus* Chamberlin); one male; Panama Cerro Flores (*Stygnommatipus rufus* Petrunkevitch) one male; Limon, Bomba 21 July 1976, one male; Puntarenas, Las Cruces near San Vito 1 August 1976, one immature male; Puntarenas, Osa Peninsula, Llorona Ridge Trail, 24 August 1979, one male, one immature; Puntarenas, Manuel Antonio National Park, 18 June 1976, one male, one female; Puntarenas, Osa Peninsula, Llorona Swamp Trail, 9 August 1978, one immature.

Remarks.—This is a widely distributed form which has been described several times. There is considerable variation in the number of tarsal segments in leg I; it may vary from 6 to 8 in this species. Though we tried to find the place of disposition of the type specimen, we were unsuccessful.

SAMOINAE SOERENSEN

Pellobunus Banks

Pellobunus Banks 1905:22, Roewer, 1912:145, 1923:111; Goodnight and Goodnight, 1947b:2. *Psyctrapus* Roewer, 1933:276; Silhavy 1979:23. **NEW SYNONYMY.**

Type species.—*Pellobunus insularis* Banks.

Diagnosis.—Phalangodids of medium size, eye tubercle slightly removed from the anterior margin of the cephalothorax, low rounded. Dorsum with five areas, first without median line, borders parallel. Spiracles partially concealed. Tarsal segments: 4-6-5-5 or 6. Distitarsus of first tarsus with two segments, second with three. Metatarsi without astraguli or calcanei; tarsal claws of legs III and IV, arising individually, with scopula. Penis a sclerotized shaft.

Remarks.—At present, only three species are known in this genus: *Pellobunus insularis* Banks from Panama and Costa Rica, *Pellobunus haitiensis* (Silhavy) from Haiti, and *Pellobunus insulcatus* (Roewer) from El Salvador. The scopula is not conspicuous in these forms and may be easily overlooked during study.

Pellobunus insularis Banks

Figs. 104-107

Pellobunus insularis Banks 1905:22, figs. 4a-d; Roewer 1912:147; 1923:111; Goodnight and Goodnight, 1947b:2, figs. 14-16.

Psycitrus metatarsalis Roewer 1933:276, fig. 1. NEW SYNONYMY.

Psycitrus panamensis Silhavy 1979:23-24, figs. 51-55. NEW SYNONYMY.

Description of male.—Total length of body, 2.4 mm; cephalothorax length, 0.9 mm; width of body at widest portion, 1.8 mm. Length of legs (I-II-III-IV in mm): Trochanter 0.2-0.2-0.2-0.3; Femur 0.9-1.8-0.8-1.0; Patella 0.4-0.4-0.3-0.4; Tibia 0.6-1.0-0.7-0.3; Metatarsus 0.8-1.1-1.1-0.8; Tarsus 0.4-1.0-0.6-0.8; Total 3.3-5.5-3.7-4.7.

Cephalothorax smooth, only a few low tubercles on and behind the eye tubercle. Eye tubercle slightly removed from the anterior margin of the cephalothorax, low, rounded above. Dorsal areas not clearly defined; dorsum with numerous low tubercles giving the surface a roughened appearance. Entire venter with numerous low tubercles which are present on coxa II as a median row and as scattered tubercles on remaining coxae. Coxa III with an anterior and posterior row of teeth-like tubercles. Each free sternite with a transverse row of tubercles. Anal operculum similarly covered. Spiracles visible, but not widely expanded.

Penis sclerotized shaft, 0.3 mm long.

Palpus: trochanter, 0.2 mm long; femur, 0.7; patella, 0.4; tibia, 0.4; and tarsus, 0.3. Total length, 2 mm. Palpus armed as in figure. The palpi and chelicerae of male are somewhat enlarged.

All segments of legs with hairs, most numerous on the tarsi. Metatarsus II with false articulations; metatarsus III with a median enlargement as in figure. The central elongate area is lighter than the remaining portion of the legs. The function of this structure is not readily apparent, possibly it has a special sensory function. Tarsal segments: 4-6-5-6. Scopulae present on tarsi of legs III and IV.

Entire body and appendages a dark reddish-brown; trochanters lighter. Some black mottlings on the dorsum, presenting a somewhat streaked appearance. The legs, particularly legs I and II are somewhat darker. Darker markings are conspicuous on the palpi. There is some variation in the markings with the specimens from Panama being somewhat darker.

Female.—Total length of body, 2.4 mm; cephalothorax length, 0.8 mm; width of body at widest portion, 1.9 mm. Similar in appearance to the male but lacking the special

structure on metatarsus III; also the chelicerae and palpi are not nearly so enlarged. Ovipositor with rounded anterior end and a few spines around the border.

Type data.—Female holotype from Cocos Island, Costa Rica (Banks' record) MCZ, examined.

Additional records.—Rio Parismina, near the Atlantic Coast, 3 May 1930 (Roewer's record for *Psyctrapus metatarsalis*), NHMS, not examined; Panama: Canal Zone, Summit Gardens, May 1964, 7 males, 6 females; May 1969, one female; Barro Colorado Island, May 1964, seven males, five females; 24 July 1936, one female (all collections by Chickering) (Silhavy's records); Barro Colorado Island, February, 1945; Juan Mina, Canal Zone, March 1945, one female (last two collections by C. D. Michener).

Records.—Though this small phalangodid is easily recognized by the unique structure on the metatarsus of leg III, it has been described three times probably due to the fact that Banks' original description was based upon a single female. In 1947, we redescribed Banks' holotype and listed two identified females from Panama. Roewer (1933) first described the male of this species from Costa Rica. Our examination of the specimens available to us has convinced us that all of them actually represent *Pellobunus insularis* Banks. This again points out the problems that arise when only females are available for study; mistakes result.

Another problem presented by this species is the assigning of it to the subfamily Samoinae. Both Roewer and Silhavy felt that there was a scopula present on tarsi III and IV; this is the main character that distinguishes this subfamily from others of Phalangodidae. We have examined all our specimens carefully, and it is indeed true that the hairs present on these tarsi are heavier and just possibly do represent a scopula. We are abiding by their decision, but reserve the right to question the accuracy of it. It appears important to us to study representatives of this subfamily from Samoa in order better to determine what does constitute true scopula.

ACKNOWLEDGMENTS

Although most of the material studied was collected by us, we do wish to thank a few individuals who kindly made their specimens available to us for study. These include Dr. Francke of Texas Tech University, Lubbock, Texas and Mr. E. Dixon whose material was loaned to us by the State Museum of Florida, Gainesville, Florida. Our son, Charles, was able to collect material from areas which he visited while a student with the Organization of Tropical Studies. We appreciate the effort he made for us.

We also had the good fortune to be able to examine many of Roewer's types from his 1949 studies through the kind offices of Dr. M. Grasshoff of the Natural History Museum of Senckenberg, Frankfurt, West Germany (NHMS). The holotype of Soeren's species, *Chersobleptes boveli* (= *Stygnoleptes analis*) was examined through the courtesy of Mr. Torbjörn Kronestedt of the Naturhistoriska Riksmuseet of Stockholm, Sweden (NRS). Dr. Herbert Levi of the Museum of Comparative Zoology (MCZ) Cambridge Massachusetts loaned us some of Banks' types. Finally Dr. Norman Platnick of the American Museum of Natural History (AMNH) sent us types of some of our species for reexamination.

We are indebted to many kind people in Costa Rica, particularly the personnel of the Organization for Tropical Studies (OTS) who helped us with advice from time to time. In particular we appreciated the fact that the government of Costa Rica has had the fore-

sight to preserve many unique areas. These present an unparalleled opportunity for the biologist to learn more about this marvelously complex and beautiful country.

Finally, we wish to thank Mr. James Cokendolpher for his many helpful suggestions in editing this manuscript.

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TERGAL AND STERNAL ANOMALIES IN *NEOBISIUM* CHAMBERLIN (NEOBISIIDAE, PSEUDOSCORPIONES, ARACHNIDA)¹

B. P. M. Ćurčić, M. D. Krunić and M. M. Brajković

Institute of Zoology, Faculty of Science
University of Belgrade
16, Studentski trg, Yu - 11000 Beograd
Yugoslavia

ABSTRACT

Traumatic (teratological and accidental) variation in the structure of the abdominal sclerites has been studied in the pseudoscorpion species *Neobisium carpaticum* Beier 1934, and *N. fuscimanum* (C. L. Koch 1843). In the former species, tergal abnormalities have been found in 0.75 - 1.33% of the samples analyzed; in the latter, tergal and sternal deficiencies have been noted in 0.97% of the sample studied. The following aberrations have been observed: hemiatrophy, hemimery, symphysomery, and enlargement of the sclerites, as well as various combinations of these anomalies. The pathomorphology and possible origin of these teratological phenomena are discussed.

INTRODUCTION

Within the pseudoscorpion family Neobisiidae, anomalies of abdominal tergites and sternites have been registered to date for the following species: *Neobisium erythrodactylum* (L. Koch 1873), *N. maritimum* (Leach 1817), *N. muscorum* (Leach 1817), *N. carpaticum* Beier, 1934, *N. sylvaticum* (C. L. Koch 1835), and *Roncus lubricus* L. Koch, 1873 (Pedder 1965; Ćurčić 1980; Ćurčić et al., in press).

In this paper, we aim firstly to express qualitatively and quantitatively the phenomenon of traumatic (teratological and accidental) variation in the structure of the abdominal sclerites in the species *N. carpaticum* and *N. fuscimanum* (C. L. Koch 1843), especially in the adult stage (males and females) in order to assess the frequency and origin of such aberrations.

MATERIALS AND METHODS

A total of 1,550 adult specimens of *N. carpaticum* from Mt. Avala, near Belgrade (1,000 specimens, 500 of each sex), Mt. Fruška Gora, near Sremski Karlovci (150 specimens, 75 of each sex), and Mt. Kosmaj, near Mladenovac, Yugoslavia (400 specimens, 200 of each sex) were collected. In addition, 310 specimens (155 of each sex) of *N. fuscimanum* from Mt. Avala, near Belgrade were examined.

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Specimens of *N. carpaticum* were collected by sieving leaf-litter of mixed oak and beach forest while specimens of *N. fuscimanum* were taken from leaf-litter of an oak forest within the period extending from September 1972 to May 1981.

The nomenclature of anomalies of the abdominal sclerites made by Balazuc (1948) was used in this paper.

RESULTS

A total of seventeen abnormal specimens were found — 14 of *N. carpaticum* and three of *N. fuscimanum*. The results of the analysis of teratological variability in the structure of the abdominal tergites and sternites of these two species are as follows:

Neobisium carpaticum

(a) Male (Fig. 1A). In this specimen, parts of tergite I and especially of tergite II are missing; there is no pigmentation in the affected area. As a consequence of this deficiency, we found a disturbance of the chaetotaxy of the first two abdominal tergites, manifested in the reduced number and unequal distribution of setae.

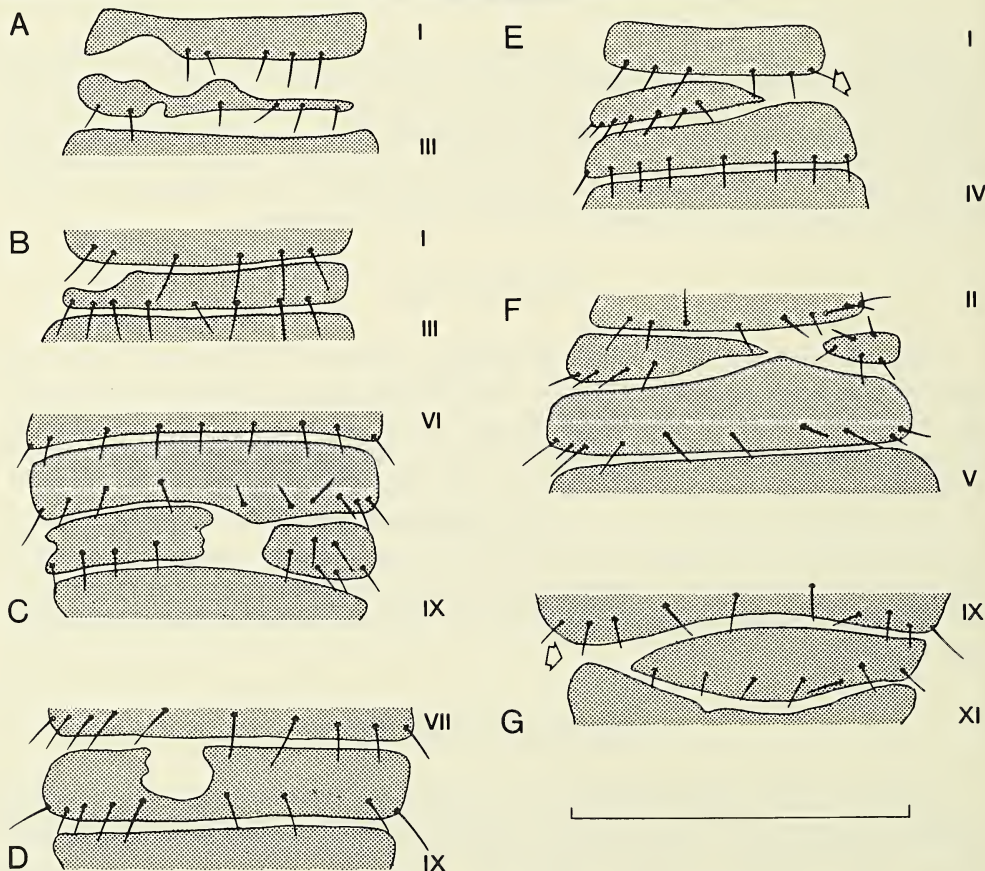


Fig. 1.—*Neobisium carpaticum* Beier 1934; scale bar = 1 mm. A, tergites I-III, male, Mt. Avala; B, tergites I-III, male, Mt. Avala; C, tergites VI-IX, female, Mt. Avala; D, tergites VII-IX, female, Mt. Avala; E, tergites I-IV, male, Mt. Avala; F, tergites II-V, male, Mt. Kosmaj; G, tergites IX-XI, female, Mt. Fruška Gora.

(b) Male (Fig. 1B). Part of the left side of tergite II is missing; this area lacks pigmentation. Despite this anomaly, the setal formula of tergite II is unaltered.

(c) Female (Fig. 1C). Tergites VII and VIII are anomalous which is more pronounced on the latter tergite. The mid-region of tergite VIII is completely absent. Although the numbers of setae on these two tergites are unchanged, their distributions deviate significantly from normal specimens - on the right side of tergite VIII, the setae are unequally distributed and are arranged in two rows. The mid-region lacks any setae. The central part of the tergite VII is enlarged backwards to fill part of the space left vacant in tergite VIII.

(d) Female (Fig. 1D). The left anterior part of tergite VIII is without pigmentation. Because of this anomaly, the setal formula of tergite VIII is altered, and the setae are concentrated on the left half of the sclerite.

(e) Male (Fig. 1E). In this specimen, the right half of tergite II is missing. The adjacent part of tergite III is enlarged and partially fills the gap left by the missing half of tergite II. The arrangement of setae on the damaged sclerite is altered, and the setae are concentrated on the left half of the tergite.

(f) Male (Fig. 1F). In this case, a deficiency is found in tergite III manifested by the absence of the mid-region of the sclerite. This anomaly has caused the unequal distribution of individual setae. On the right, the setae are concentrated on the small section of tergite III where they are arranged in two rows. Tergite IV is enlarged in its mid-region and fills the central space where the missing part of tergite III would otherwise be found.

(g) Female (Fig. 1G). Part of tergite X on the left is missing, and thus tergite IX touches tergite XI directly in this region. In addition, the number of setae on the sclerite is reduced compared with the values which have been quoted for *N. carpaticum* (Ćurčić 1977).

(h) Male (Fig. 2A). Tergites III and IV are fused from the left side to the mid-region. Thus the relative distribution of the setae on tergite III is altered and does not correspond to that accepted for *N. carpaticum* (Ćurčić 1977).

(i) Male (Fig. 2B). In this case, tergite IV and V have partially fused both from the right side to the mid-region. The number of setae on tergite IV is reduced, and the setal distribution is unequal.

(j) Male (Fig. 2C). Tergites VI and VII are fused in the mid-region. Apart from this, there is a reduction in tergite VI which resulted in the existence of a small isolated tergal section on the right. The region in which fusion has taken place (tergite VI) as well as the mid-region of tergite VII are free of setae, and thus their number is lower than the values quoted elsewhere for *N. carpaticum* (Ćurčić 1977).

(k) Male (Fig. 2D). Tergites VI and VII of this specimen are also fused in the mid-region. The setal formula shows a reduction in the number of setae on both tergites, and the position of the setae are altered (the central tergal region lacks setae).

(l) Male (Fig. 2E). In this specimen, tergites VIII and IX are fused for almost their whole length, except for one part on the left side. As a consequence, the setae on tergite VIII are few in number and unequally distributed, as well as being completely lacking in the mid-region.

(m) Male (Fig. 3). In this case, the tergal abnormalities affect five tergites. The deficiencies on tergites II-V are manifested as follows: the left half of tergite II and III are missing, with two small irregularly-shaped tergal sections on the damaged side. The consequence of this anomaly is that tergite IV is enlarged in its left part. There is a direct correlation between changes in the segmentation of the abdominal tergites II and III and

changes in their chaetotaxy; these are manifested primarily in the reduced number of setae and in their unequal distribution compared with the normal situation in *N. carpaticum*.

Another interesting anomaly in the same specimen is found in tergite VII and VIII. First of all, the mid-region of tergite VII is missing: this region has no pigmentation. Besides this, tergites VII and VIII are fused in the mid-region. As a result of this anomaly, the number of setae in the mid-region of the tergite VII is reduced, whereas the distribution of the setae is altered compared with the values quoted elsewhere for *N. carpaticum* (Ćurčić 1977).

(n) Male (Fig. 4). The posterior tergites of this specimen (IX-XI) are partially fused on the left (Fig. 4A). This deficiency has caused a disturbance in the distribution of setae on tergites IX and X, and on tergite X, the total number of setae is less than in normal specimens.

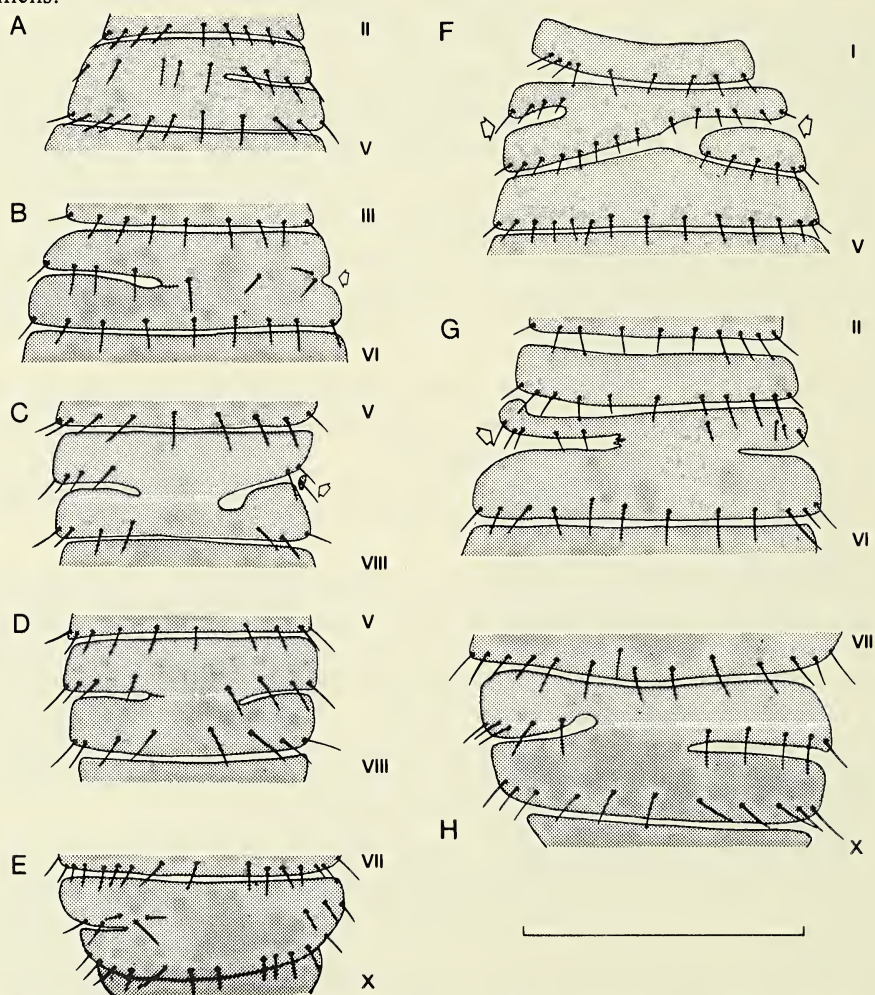


Fig. 2.—*Neobisium carpaticum* Beier 1934 (A-E) and *N. fuscimanum* (C. L. Koch 1843) (F-H); scale bar = 1 mm. A, tergites II-V, male, Mt. Fruška Gora; B, tergites III-VI, male, Mt. Avala; C, tergites V-VIII, males, Mt. Avala; D, tergites V-VIII, male, Mt. Avala; E, tergites VII-X, male, Mt. Avala; F, tergites I-V, males, Mt. Avala; G, tergites II-VI, male, Mt. Avala; H, tergites VII-X, male, Mt. Avala.

In the same pseudoscorpion there are similar changes on the ventral part of the abdomen (Fig. 4B). In this case, sternites IX and X are fused on the left side. It is obvious, however, that sternite X is narrowed on the left side which is otherwise linked with the previous sclerite. This abnormality has not caused corresponding alternations in the setal formula of the sternites.

Neobisium fuscimanum

(o) Male (Fig. 2F). It is interesting to note the teratological changes on tergites II-IV of this specimen. Thus tergites II and III are fused on the left, with the left half of tergite III fused with the mid-region of tergite II. Hence the right half of tergite III (right demi-tergite) is isolated and is not linked with the other part of the same tergite. Tergite IV is enlarged and fills the region between left and right demi-tergite III.

As a result of these changes, the chaetotaxy of tergites II and III is altered, particularly in relation to the number and relative arrangement of the setae.

(p) Male (Fig. 2G). Tergites IV and V are deficient. Tergite IV is significantly narrowed and is joined in its mid-region with tergite V. The consequence of this anomaly is seen in the irregular chaetotaxy of tergite IV; that is, in the lower number of setae and their altered distribution.

(q) Male (Fig. 2H). Tergites VIII and X are fused in the mid-region. This teratological phenomenon has resulted in this region of tergite VIII being deprived of setae.

DISCUSSION

In the specimens of *N. carpaticum* studied, tergal abnormalities were found in 0.75% of the cases in the sample from Mt. Kosmaj, in 0.90% of the cases in the sample from Mt. Avala, and in 1.33% of the cases in Mt. Fruška Gora sample. The absence of any tergal and sternal abnormalities in the subadult stages (Čurčić et al., 1981) shows that these anomalies originate during the maturation molt; that is, at the transformation of tritonymph into adults.

Of a total of fourteen specimens of this species with tergal and sternal anomalies, twelve specimens (or 86%) are males and only two are females (14%). It is clear from earlier studies (Čurčić and Dimitrijević, in press) that various tergal and sternal deficiencies in *N. carpaticum* occur mainly at the maturation molt of tritonymphs into males; the results of the present analysis support the above opinion, since the majority of abdominal anomalies occur in the male. The reason for this phenomenon is still unclear.

Tergal and sternal anomalies in *N. fuscimanum* were found in three specimens or 0.97% of the sample from Mt. Avala. As in the preceding species, the abnormalities of the abdominal sclerites are restricted to males. It remains to be confirmed on the basis of analysis of a larger number of examples among species from different locations whether the (male) sex-linked nature of the origin of the abdominal anomalies is characteristic only of certain taxa of pseudoscorpions, or whether it is universally valid for representatives of the Neobisiidae and other families.

In *N. carpaticum* (Fig. 1A), atrophy of sections of tergites II and III were discovered; this anomaly resulted in disruption of the number and distribution of setae of both tergites. Partial atrophy of tergite II was also found in the following case (Fig. 1B), but the tergal chaetotaxy was not changed. In another example of the same species (Fig. 1C), the tergal anomaly can also be characterized as partial atrophy of tergite VIII, in which the mid-region of this sclerite is missing. The chaetotaxy of the right section of the same

tergite is significantly disturbed. Apart from this, the preceding tergite is enlarged in its mid-region and partially fills the space left by the missing part of tergite VIII. A similar phenomenon is also noted in the following specimen (Fig. 1D).

Apart from tergal atrophy, the defective specimens (Fig. 1E-G) are also characterized by the presence of hemimery (or partial atrophy ?) of a tergite and enlargement of an adjacent tergite that partially fills the space left by the missing part of the damaged tergite. In all three cases quoted (Figs. 1E-G), as a result of the anomalies, the chaetotaxy of affected tergites is disturbed and does not correspond to that recorded for normal *N. carpaticum* (Ćurčić 1977).

In *N. carpaticum*, symphysomery has been discovered, in which two adjacent tergites were fused in the middle (Figs. 2C and 2D), on the left (Fig. 2A), or on the right side (Figs. 2B and 2E). In all of these specimens, the setal formula of the specimen of *N. carpaticum* (Fig. 2C), partial atrophy of the sclerite was found in addition to the symphysomery which affected tergites VI and VII.

Considerably more complex damage was found in the male of the same species from Mt. Fruška Gora (Fig. 3). In this case, deficiencies were observed in as many as five tergites; they include hemimery, partial atrophy, and symphysomery as well as enlargement of part of the sclerite (left demi-tergite IV).

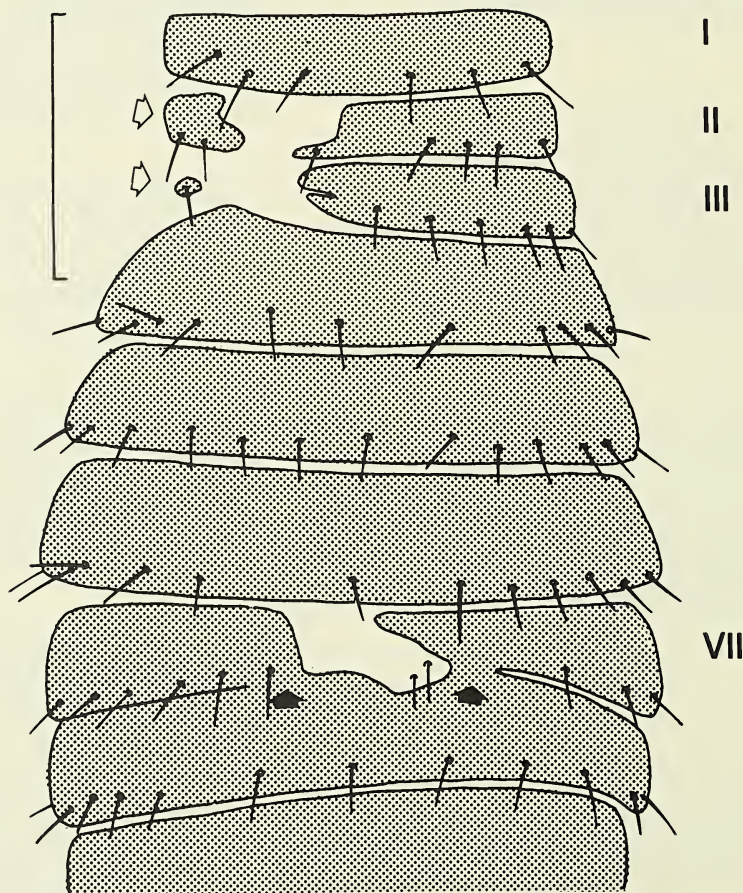


Fig. 3.—*Neobisium carpaticum* Beier 1934, male, Mt. Fruška Gora; scale bar = 0,5 mm. Tergites I-X.

The only case of anomaly in the structure of the sternites (symphysomery) was recorded in a male of *N. carpaticum* from Mt. Kosmaj (Fig. 4B). This abnormality is correlated with the phenomenon of symphysomery of tergites IX-XI of the same specimen (Fig. 4A). In this pseudoscorpion, the setal formula of the damaged tergites were considerably disturbed, but not of the sternites.

In *N. fuscimanum*, cases of symphysomery and combinations of symphysomery and partial atrophy and of symphysomery and helicomery were noted. In the first case (Fig. 2H), the tergites were fused in the mid-region, as was the case with the second specimen (Fig. 2G), where the anterior fused sclerite was also partially atrophied. In the third case (Fig. 2F), the tergites were partially fused on the left, with the right half of one tergite fusing with the left half of the adjacent tergite (dextral monocyclical helicomery). In addition, the anteromedian part of the adjacent tergite IV was enlarged. In all of these instances, the chaetotaxy of the tergites differs from that of normal specimens (Ćurčić 1977).

Analysis of teratological variability has shown that in *N. carpaticum* and *N. fuscimanum* the phenomenon of symphysomery is manifested on tergites III-X, with maxi-

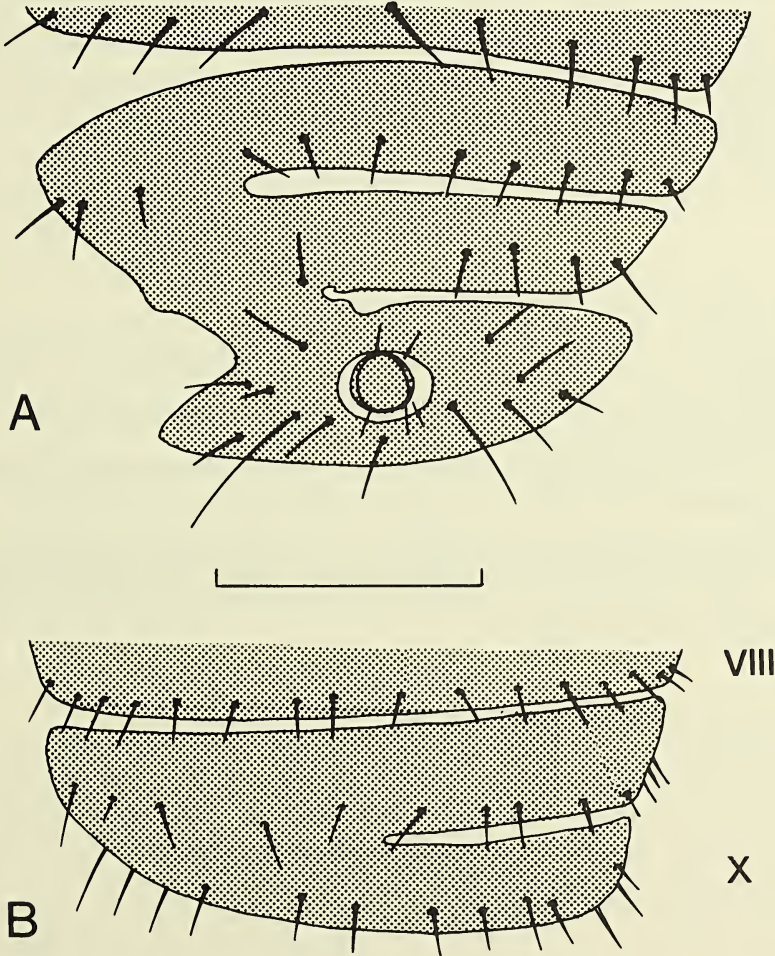


Fig. 4.—*Neobisium carpaticum* Beier 1934, male, Mt. Kosmaj; scale bar = 0,5 mm. A, tergites VIII-XIII; B, sternites VIII-X.

imum frequency on tergites IV and VII-X. Hemiatrophy and hemimery, however, affect the anterior (I-III) and posterior tergites (VII-X), which corresponds with the conclusion drawn by Ćurčić and Dimitrijević (in press). The maximum frequency of three phenomena is found in tergite II. Helicomery occurs most rarely of all and was found in only one case and on tergites II and III. Sternal aberration (symphysomery) was also observed in a single specimen of *N. carpaticum*, affecting sternites IX and X.

In *N. fuscimanum*, three cases of symphysomery were registered, two of these in combination with helicomery and partial atrophy, whereas the occurrence of other types of tergal anomalies was not established.

The majority of abnormalities observed in the tergal and sternal structures of the pseudoscorpions *N. carpaticum* and *N. fuscimanum* are the result of changes which probably took place at the last molt. A small number of the anomalies seen, however, could have arisen as the result of mechanical damage to the tergites at one of the earlier developmental stages.

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SMERINGURUS, A NEW SUBGENUS OF PARUROCTONUS WERNER (SCORPIONES, VAEJOVIDAE)

Richard M. Haradon

9 High Street
Stoneham, Massachusetts 02180

ABSTRACT

Paruroctonus Werner consists of two sympatric subgenera, the nominate and *Smeringurus*, new subgenus. *Smeringurus* is defined by the presence of numerous short setae on the ventral intercarinal surfaces of metasomal segments I-IV, and by having a significantly more slender metasoma. *Smeringurus* consists of four species endemic to the southwestern deserts of North America: *P. vachoni* Stahnke (type species), *P. mesaensis* Stahnke, *P. grandis* (Williams), and *P. aridus* Soleglad. Two subspecies of *P. vachoni* are defined by the numbers of primary denticles on the grasping edge of the pedipalp fingers: *P. v. vachoni*, from the northern Mojave Desert region, and *P. v. immanis* Soleglad, new combination, from the central and southern Mojave Desert and the Colorado Desert. *Paruroctonus vachoni*, *P. grandis* and *P. aridus* are allopatric, occupying rocky substrates; each occurs sympatrically with *P. mesaensis*, a psammophilous species.

INTRODUCTION

Within the North American scorpion genus *Paruroctonus* Werner, 1934, is a distinct element that includes *Paruroctonus vachoni* Stahnke, 1961, and four other nominal species. Soleglad (1972) described two of these species, and discussed for the first time the distinctive characteristics of the group. Stahnke (1974) doubted the status of both of Soleglad's species, implicitly, by omitting them from a list of what Stahnke considered to be the valid *Paruroctonus* species. The purposes of this report are to evaluate new and previously employed taxonomic characters, clarify the status of each nominal species, and to propose a subgeneric name for this species group.

METHODS

The measurements I have used are those standard in scorpion systematics, with the difference from some workers of the definition of pedipalp chela width. For this measurement, I have followed Stahnke (1970:304), measuring the greatest width from the inner secondary carina to the exterior marginal carina (= inner and outer carinae respectively in Soleglad 1973:354, 355, figs. 1-12). This is invariably the widest measurement on the chela at any point of rotation, and does not correspond to the width of the chela observed dorsally on a live animal in repose.

To reduce any allometric influence upon the sample distributions of morphometric ratios, the raw data for each sample were first sorted into three size groups. The carapace

length provides an adequate estimate of maturity where ratios are involved, and requires a single measurement that can be made with reasonable precision, and which relates directly to the usual series of comparative measurements and ratios. It is used in preference to the total length of the scorpion, a precise measurement of which involves the summation of 14 lengths, including the often difficult measurement of each tergite. Specimens with a carapace shorter than 5.0 mm were designated as immatures. Specimens with a carapace equal to or longer than 5.0 mm, but which were not yet adults, were designated as juveniles. Adults were determined primarily by the development of scalloping, distinct or subtle, along the grasping edge of the pedipalp fingers. In determining adult females it was usually necessary to consider such scalloping in relation to the coloration of the cuticle (which tends to be somewhat darker in adults), and to the carinal granulation (which tends to be coarser in adults).

The rows of primary denticles (Fig. 2) on the pedipalp fingers are numbered 1 (distal) to 6 (proximal), after Williams (1980:2). The numbers of primary denticles in rows 1-5 are used to define subspecies, and are reported as the whole number nearest each sample mean, in the manner 1/2/3/4/5. The denticle counts exclude the enlarged denticles that delimit the six rows.

Statistical data are given as: mean $\pm$ one standard deviation; n = sample size; d.f. = degrees of freedom.

DIAGNOSTIC CHARACTERS

The species considered herein are defined by unique developments in one or more, or by a unique combination of developments in all four, of the following characters: (1) The scalloping of the grasping edge of the pedipalp fingers in adult males, (2) number and pattern of setae on the basitarsus of legs 1-3, (3) number of ventrolateral setae on metasomal segment V, and (4) the basic pattern of fuscous pigmentation. Two subspecies are defined by the numbers of primary denticles on the pedipalp fingers. Each of the other diagnostic characters used herein consists of two or more distinct, but not always unique, states of development. To correctly identify specimens, the variability of the characters might require that the entire series of diagnostic criteria given for each taxon be evaluated.

1. Scalloping of adult male pedipalp fingers. Three characteristic developments are recognized. The first two are exemplified by Figures 4 and 6. The range of variability of the third condition is shown by Figures 8 and 10.

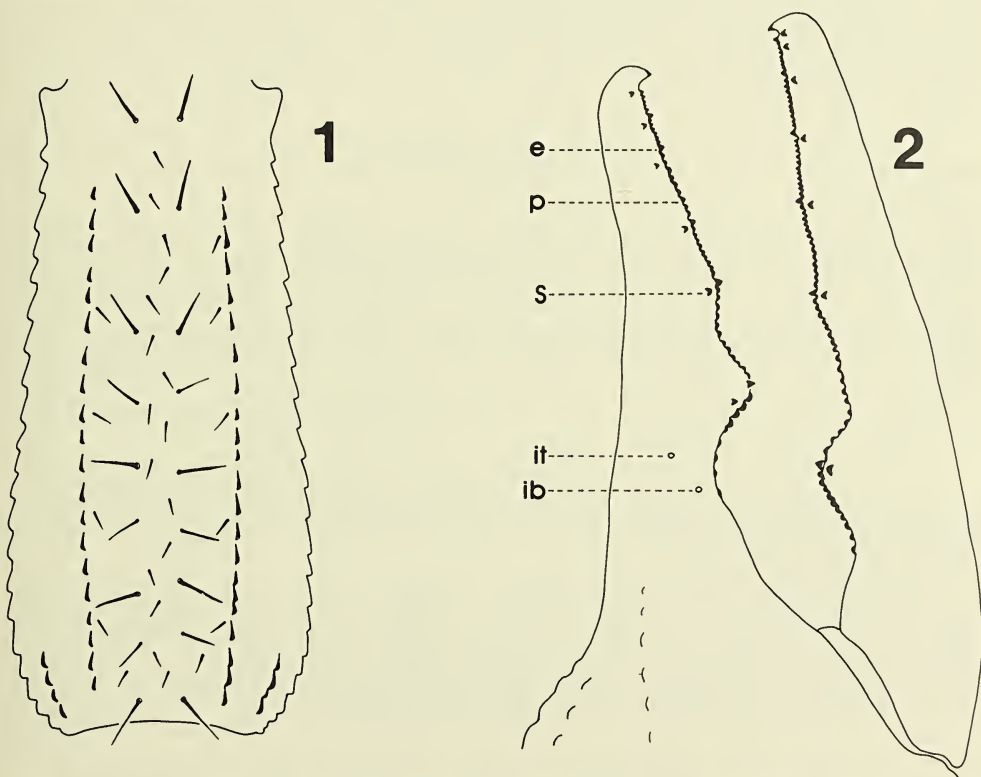
2. Leg setae. In *P. mesaensis* there are typically nine or more very long setae in an essentially even series along the retrolateral surface of the basitarsus of the third pair of legs (Fig. 17). The other three species in the subgenus bear eight or fewer, irregularly positioned, short and moderately long setae along the retrolateral surface (Fig. 16). There is a similar, but less conspicuous, difference between *P. mesaensis* and the other three species in the setation of the first two pairs of legs, as well.

Heretofore, tarsal setae otherwise have been ignored as taxonomic characters in *Paruroctonus*, and in the family Vaejovidae generally. The minute setae which form three inferior rows (one each more or less in line with, and one between, the prolateral and retrolateral pedal spurs, or calcars) on the basitarsus of legs 1-3 are herein referred to as spinules. Three of the four species in the subgenus bear on legs 1-3 a stout bristle at about mid-length of the basitarsus along the inferior retrolateral row of spinules (Fig. 18). The bristle is distinctly stouter than any, and shorter than most, of the large setae in the

retrolateral series. *Paruroctonus mesaensis* lacks this bristle on legs 1 (Fig. 19) and 2.

3. Metasomal setae. There are typically eight pairs of ventrolateral setae on metasomal segment V in all the species of the subgenus except *P. mesaensis*. The number in *P. mesaensis* usually ranges from 10 to 14. In all the species the number of setae varies from loss, or by the presence of extraneous setae that are usually smaller and offset from the main series. Immatures typically lack two or more setae from the full complement exhibited by juveniles and adults. The development of the dorsal metasomal setae I-IV varies among the species, and in some species among populations.

4. Fuscous markings. In this study I have distinguished between the basic carapacial and tergal pattern, or design, that might characterize a species, and the relative intensity, or darkness, or that pattern which various specimens or populations might exhibit. With rare exceptions, *P. mesaensis* entirely lacks fuscosity, and thus presents a dichotomy generally reliable in distinguishing that species from the other species in the subgenus, all three of which exhibit unique basic patterns of fuscosity on the carapace and tergites. Conspicuous differences occur in the quantity of melanin present within and among populations, but such differences represent tendencies along a common gradient and are not considered important taxonomically. There is, apparently, a correlation between the amount of fuscosity present and the darkness of the local substrate. (See "Remarks" under *Paruroctonus vachoni immanis* Soleglad below).



Figs. 1-2.—1, *P. mesaensis*, ventral aspect of metasomal segment III, showing large paired carinal setae, and smaller intercarinal setae; 2, *P. vachoni*, interior aspect of adult male pedipalp fingers, showing enlarged (e), primary (p) and supernumerary (s) denticles, and *ib* and *it* trichobothrial positions.

5. Dentition of pedipalp fingers. The numbers of primary denticles in rows 1-5 on the grasping edge of each pedipalp finger are not clearly discernible until about the second instar. The number of denticles in row 6 on the fixed and movable fingers increases during the first two, and probably the third, instars. Although the denticles are subject to considerable wear, damage, and occasional loss, these conditions are rarely an obstacle to identifying taxa. The numbers of denticles in rows 1-5 show no evidence of sexual dimorphism. The number of denticles in row 6 of adult males is correlated with the extent of scalloping on the fingers, and can be useful for diagnosing three of the four species in the subgenus. The possible error in row 6 counts (see below) makes subtle differences observed between subspecies of doubtful value, and the counts are omitted here.

A correlation was found in the numbers of denticles among various rows, and thus has a bearing on the usefulness of the counts as diagnostic characters. For example, in a sample of *Paruroctonus grandis* (Williams) ($n = 246$), tests for independence (chi square analysis) in various numbers of denticles between row 1 and each of rows 2 through 5 on the same movable finger indicated that the counts in the first three rows were not independent (rows 1 and 2, $\chi^2 = 50.18$, d.f. = 21, $P < 0.01$; rows 1 and 3, $\chi^2 = 40.09$, d.f. = 21, $P < 0.01$; rows 1 and 4, $\chi^2 = 30.92$, d.f. = 21, $P > 0.05$; rows 1 and 5, $\chi^2 = 30.78$, d.f. = 33, $P > 0.05$). Similar correlations were observed in counts on the fixed finger of *P. grandis*, and on the fingers of other taxa, as well.

In the same *P. grandis* sample there was a significant correlation between the counts (sum of rows 1-5) on the fixed and movable fingers on the same chela ($r = 0.636$, $n = 257$). The sum of rows 1-5 on the left and right fixed fingers, and the left and right movable fingers, were more than 95% of the time asymmetrical. On each chela the movable finger always bore more denticles (sum of rows 1-5) than the fixed finger.

The denticle counts in row 6 on the movable and especially the fixed fingers are among the more variable. Obtaining exact counts in row 6 is often hampered by the gradual reduction in size and obsolescence of the denticles toward the articular membrane. This is particularly so among mature males of *Paruroctonus vachoni* Stahnke, which typically lose 50% or more of the juvenile complement from row six on the fixed finger, and usually two to four denticles from the juvenile series on the movable finger. Mature male *P. grandis* typically lose about 33% of the juvenile series from the fixed finger; there is no significant loss on the movable finger. In adult males of *P. vachoni* and *P. grandis* there are seldom more than 12 large denticles in series on row 6 before there is an abrupt reduction in size, and increase in spacing, of the denticles.

6. Pigmentation of pedipalp fingers. In species having darkly pigmented pedipalp fingers, the pigmentation usually becomes distinct among late immatures. The color, and the contrast between the fingers and the palm, observed in live specimens is often obscured in preserved material.

7. Trichobothria. The most significant variability evident within the subgenus involves the digital series. The position of *ib* on the fixed finger (Fig. 2) is indicative of the relative positions (distal or proximal) of the remaining digital trichobothria. The position of *ib* is measured by the ratio, fixed finger length/distance *ib* to finger tip. This ratio increases as the scorpion matures, lending the appearance of ontogenetic "migration" of *ib* distally. There is also significant variation in the position of *ib* among species and subspecies, and among some populations of *P. vachoni* and *P. mesaensis*.

8. Metasomal carinae. The development and granulation of the ventral and ventrolateral carinae on metasomal segments I-III are directly correlated, the latter generally being more sharply defined and somewhat more granular. Only the ventral carinae are

referred to diagnostically. Sexual dimorphism and intraspecific variability can be considerable, and differences between species are often obscured. Two states of adult development are used diagnostically; smooth and granular.

9. Morphometric ratios. Although a number of ratios were found to differ significantly ($P < 0.05$) between taxa, due to overlapping ranges of variation, few ratios permitted as much as 90% separation of taxa.

10. Pectinal tooth counts. There was little or no difference observed in the numbers of pectinal teeth among the species of the subgenus. Within a species, significant differences in the means occur among certain populations.

11. Adult size. Adults were determined as outlined in "Methods" above. In the paratopotypic sample of *P. grandis* ($n = 261$), the 20 longest carapaces among females averaged 1.15 times greater than the 20 longest carapaces among males. The slightly larger average adult size attained by females in this sample supports a general impression perceived in the course of examining these and other specimens that in the subgenus adult females are generally larger than adult males. Whether females attain maturity within a larger size range than males do is not certain.

Polis and Farley (1979b:527) defined mature *P. mesaensis* males by inference, according to a sudden divergence from the linearity shown by earlier instars in the correlation between the logarithmic growth rates of the pectines (dentate margin length) and the distance between the median eyes and the anterior margin of the carapace. It is uncertain, though, whether the point of deviation from prior linearity indicates maturity or only another step toward maturity. It is impossible to interpret the point or region of female maturity from the same graph, in which females are represented by a single straight line.

Smeringurus, new subgenus

Fig. 1

Paruroctonus (in part): Stahnke 1957:253, 1965:262, 263, 1974:119 (key), 136; Williams 1972:2, 1974:15 (key), 1980:4 (key), 31; Soleglad 1972:71, 1973:351, 353, 359, figs. 13, 14; Sissom and Francke 1981:93, 102.

Vejovis (*Paruroctonus*) (in part): Gertsch and Allred 1965:4, 9; Gertsch and Soleglad 1966:2, 3, 1972:553, 559; Williams and Hadley 1967:103, 112; Williams 1968a:7, 1968b:313, 1970a:7, 1970b:277.

Vaejovis (*Paruroctonus*) (in part): Hjelle 1972:20, 26.

Vaejovis (in part): Diaz-Nájera 1975:3, 6.

Type species.—*Paruroctonus vachoni* Stahnke, 1961.

Diagnosis.—Subgenus of genus *Paruroctonus*; species bearing numerous short setae on the ventral intercarinal surfaces of metasomal segments I-IV (Fig. 1); setae between ventral metasomal carinae I-IV total 20 or more in adults and juveniles, 10 or more on immatures with a carapace 4.0-5.0 mm long, five or more on immatures with a carapace 2.5-3.9 mm long (apparently second instars and earlier); all metasomal segments longer than wide, except in very early instars; segment III length/width in adult males greater than 2.00, in adult females greater than 1.90, in immatures of both sexes greater than 1.70.

The intercarinal metasomal setae are often inconspicuous in early instars, but when discernible on any specimen are slightly to conspicuously shorter than the paired setae positioned along the ventral carinae. Individual intercarinal setae occur only rarely among individuals belonging to the nominate subgenus.

Description.—Carapace length of adult males 6.5-10.4 mm, adult females 7.0-11.7 mm; total length of adults (including telson) about 60-100 mm; carapace length represents about 11-13% of total length in juveniles and adults. Anterior margin of carapace in adults with subtle medial concavity; on immatures and some juveniles and young adults straight to convex. Median ocular tubercle width/carapace width at mid-length, adults 0.25-0.33 (usually nearer 0.33), immatures and juveniles 0.33-0.45. Chelicerae: on movable digit, superior distal tine subparallel to, and $1/2$ (rarely less) to $2/3$ length of, inferior distal tine; three to eight (usually four to six) well developed denticles, often worn to crenulations, on inferior margin; on fixed digit, inferior margin near bicusps with one to four, usually pigmented, denticles. Chelae with all eight carinae well developed, moderately to coarsely granular (see Soleglad 1972:fig. 7). Pedipalp fingers (Fig. 2): six supernumerary denticles on fixed finger, seven on movable finger; primary denticles divided into six rows by five and six enlarged denticles on fixed and movable fingers respectively; sum of primary denticles in rows 1-5, 38-69 on fixed finger, 55-91 on movable finger. Leg 2 basitarsus with three stout bristles (excluding variably developed distal bristle) along inferior prolateral series of spinules. Pectines extend beyond distal margin of trochanter on adult males, to or beyond mid-length of trochanter on adult females; carapace length/pectine length, adult males less than 1.00, adult females less than 1.10; middle lamellae in two rows; teeth on males 28-40 (30-35 more than 95% of the time), females 20-29 (22-26 more than 90% of the time). Paired metasomal setae counts on segments I-IV: dorsolateral setae 0,2,2,3; ventrolateral setae 3,5,5,5; ventral setae usually from 3,3,3,4 in early instars, becoming 3,4,4,5 to 4,5,5,7 or more in juveniles and adults.

Subordinate taxa.—*Paruroctonus mesaensis* Stahnke, 1957; *Paruroctonus vachoni vachoni* Stahnke, 1961; *Paruroctonus vachoni immanis* Soleglad, 1972, new combination; *Paruroctonus grandis* (Williams, 1970b); *Paruroctonus aridus* Soleglad, 1972.

Distribution.—Deserts of southern California, southwestern Nevada, western and southwestern Arizona (U.S.A.), northeastern Baja California and northwestern Sonora (including several Gulf of California islands), Mexico.

Etymology.—*Smeringurus* (masculine) is derived from Greek combining forms, and refers to the ventral intercarinal metasomal setae by which this subgenus is defined.

Remarks.—*Smeringurus* is herein assigned subgeneric rank for two reasons. First, the present definitions and relationships of the several nominal vaejovoid genera are not at all clear, and placement among such poorly defined concepts poses problems that go beyond the intent or proper scope of this report. Second, although the presence of ventral intercarinal metasomal setae is apparently unique within Vaejovidae, with the exceptions of that and of having a relatively slenderer metasoma, *Smeringurus* is morphologically subordinate to the generic concept of *Paruroctonus*. Although other characteristics in combination also distinguish *Smeringurus* from the nominate subgenus, each characteristic represents only a general tendency toward one end of a modification series shared by all species in the genus.

The proposed subgenera of *Paruroctonus* are based upon first hand studies of all the nominal, and several undescribed, species in the genus. That significant phylogenetic divergence has occurred at several levels (species, species group, subgenus) within the genus is indicated by three observations. First, *Smeringurus* and the nominate subgenus are sympatric throughout the lesser range of the former. Second, within the nominate subgenus are two major species groups that are widely sympatric. Third, certain species of each species group within the nominate subgenus coexist with one another, as well as with species belonging to *Smeringurus*.

Paruroctonus vachoni Stahnke

Figs. 3, 4, 11, 12, 15, 16, 18

Paruroctonus vachoni Stahnke 1961:206-212, 1974:138, tbl. 4; Williams 1972:3, 1976:2; Soleglad 1972:72 (key), 75, 1973:355, tbl. 2; Haradon 1974:26.

Vejovis (Paruroctonus) vachoni: Gertsch and Allred 1965:9; Gertsch and Soleglad 1966:6 (key), 23-26, figs. 14, 15, 22, 49-51, 64, 66, tbl. 3; Williams 1970b:277, 281.

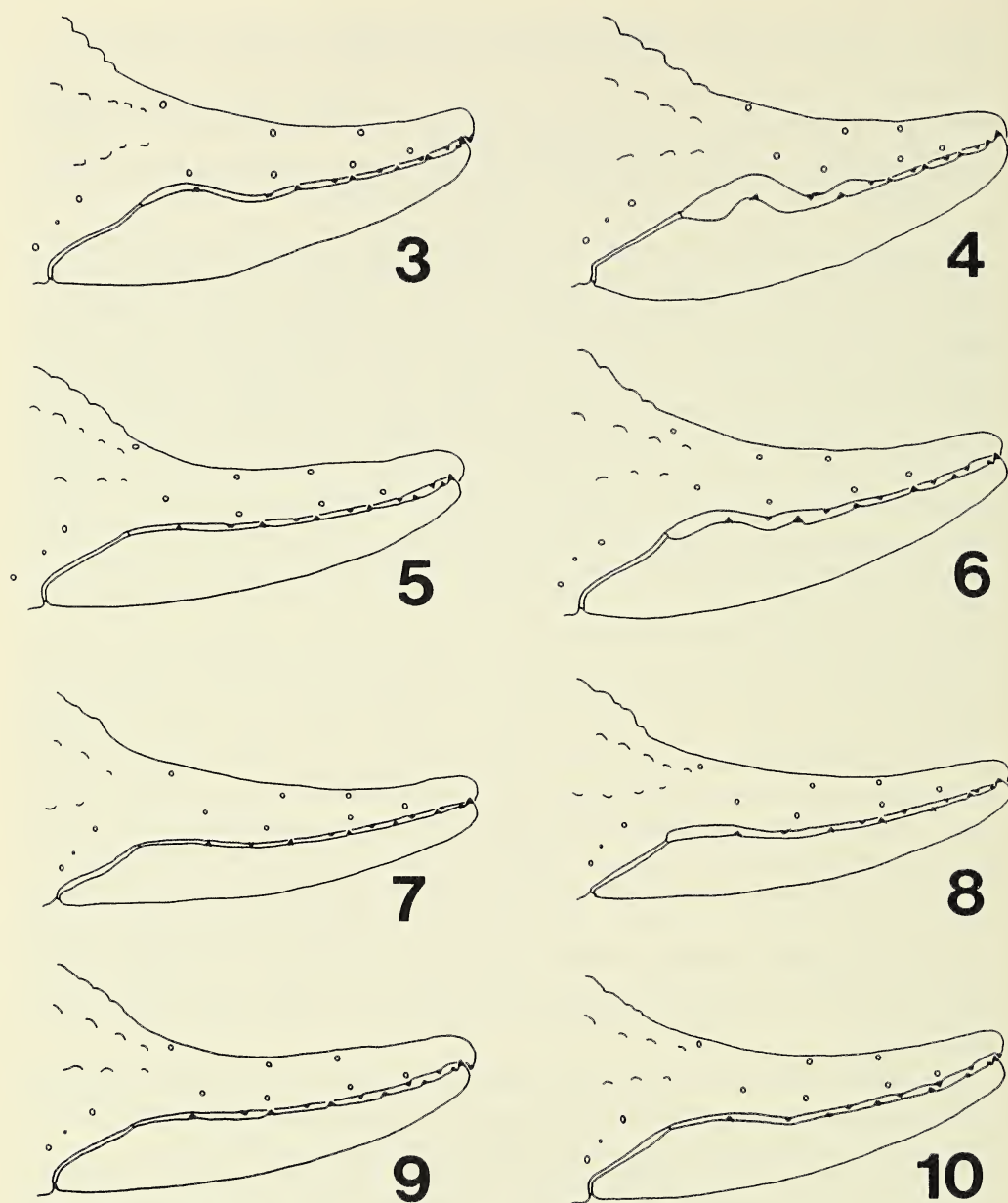
Diagnosis.—A species of subgenus *Smeringurus*; adult males with deeply scalloped pedipalp fingers, closed fingers form prominent proximal gap (Fig. 4), 15 or fewer primary denticles in row 6 of fixed finger; legs 1 and 2 with large bristle at mid-length of basitarsus along inferior retrolateral row of spinules (Fig. 18); eight or fewer irregularly positioned retrolateral setae on basitarsus of third pair of legs (Fig. 16); eight pairs of ventrolateral setae on metasomal segment V; dorsal setae on metasomal segment II about as long as dorsal setae on segments III-IV; fuscous markings usually distinct and extensive, extend into most or all of the interocular triangle (Fig. 11) and to the entire posterior margin of tergites 1-6 (Fig. 12); juveniles and adults with light to dark reddish or reddish-brown pedipalp fingers, fingers darker than yellowish or yellowish-orange palm; ventral carinae on metasomal segments I-III granular in males, at least crenulate posteriorly in females; chela length/width, less than 2.95 in adult males; telson depth/metasomal segment V width, in adults greater than 0.96.

Variation.—The scalloping and resulting proximal gap on the pedipalp fingers in adult males varied from what is shown in Figure 4 to a slightly more deeply scalloped state, especially in large males. The pedipalp fingers on adult females were weakly scalloped, and when closed formed at most a narrow proximal gap (Fig. 3); fingers were essentially unscalloped on immatures and juveniles. The cuticle varied from pale yellow to pale dusky orange. Fuscous markings on the carapace and tergites were most clearly defined on immatures and juveniles. At least vestigial markings were present on the carapace and usually the tergites of adults. In all specimens except early instars the fingers were darker than the palm. Primary denticles in row 6 of the fixed pedipalp finger in adults varied 2 to 18; counting only the larger contiguous denticles of similar size, the number seldom exceeded 12. Chela length/width, among adult males 2.71 ± 0.14 , $n = 17$; adult females 2.78 ± 0.14 , $n = 44$. Telson depth/metasomal segment V width, among adults 1.05 ± 0.07 , $n = 60$.

Distribution.—(Fig. 15). Rocky desert habitats from the northern Mojave Desert in California and adjacent areas of Nevada, south into the Colorado Desert to the U.S.A.-Mexico border, remaining north and east of the Imperial Valley of California.

Remarks.—Stahnke (1961:206) originally described *P. vachoni* as having "a carapace that has a somewhat light yellow interocular triangle followed by a darker posterior portion." In some specimens that I have studied, the interocular area appeared somewhat lighter than the rest of the carapace due to a thinner distribution of fuscosity. In some specimens the fuscosity did not extend to the anterior margin. However, in all known populations of *P. vachoni* most of the interocular area is occupied by fuscosity that is readily discernible up to at least the juvenile stage, and in most specimens into the adult stage.

Two subspecies of *P. vachoni* are distinguished by the numbers of primary denticles in rows 1-5 on the pedipalp fingers. In the samples studied, approximately 96% separation of the two subspecies was possible by comparing each specimen to the mean denticle counts of Death Valley area samples and Coachella Valley - Imperial Valley samples.



Figs. 3-10.—Pedipalp fingers, adult state, exterior aspect: 3, *P. vachoni*, female; 4, *P. vachoni*, male; 5, *P. grandis*, female; 6, *P. grandis*, male; 7, *P. aridus*, female; 8, *P. aridus*, male; 9, *P. mesaensis*, female; 10, *P. mesaensis*, male.

Along the Colorado River, particularly in Arizona, the distinction between the two subspecies is obscure (see discussion below).

Paruroctonus vachoni vachoni Stahnke

Fig. 15

Paruroctonus vachoni Stahnke 1961:206-212, 1974:138, tbl. 4 (in part); Williams 1972:3 (in part), 1976:2 (in part); Soleglad 1972:72 (key), 75 (in part), 1973:355, tbl. 2 (in part).

Vejovis (Paruroctonus) vachoni: Gertsch and Allred 1965:9 (in part ?); Gertsch and Soleglad 1966:6 (key), 23-26, figs. 14, 15, 22, 49-51, 64, 66, tbl. 3 (in part); Williams 1970b:277, 281 (in part).

Types.—*Paruroctonus vachoni*: Holotype female from U.S.A., California, San Bernardino County, Sheep Creek Springs, 37 miles N Baker (1800 ft.), 4 December 1960 (R. L. Swett). Allotype from same locality, 21 November 1960 (collector not reported). Depository: H. L. Stahnke collection, Tempe, Arizona.

Diagnosis.—Primary denticle counts in rows 1-5 closer to 6/7/9/10/12 (not 7/8/11/11/13) on fixed pedipalp finger, and 8/10/12/12/19 (not 9/11/13/13/19) on movable pedipalp finger (Table 1); from Inyo County and extreme northern San Bernardino County in California, and southwestern Nevada.

Variation.—Of more than 200 specimens examined, only one (Saline Valley, Inyo County) essentially lacked distinct fuscosity. Adult carapace length, males 7.8-10.4 mm, females 8.3-11.7 mm. Pectinal tooth counts are given in Table 2. Fixed finger length/distance *ib* trichobothrium to finger tip, adult males 1.37 ± 0.04 , $n = 26$; adult females 1.34 ± 0.04 , $n = 30$.

Distribution.—(Fig. 15). Rocky canyons and slopes, northern Mojave Desert region.

Remarks.—The "Trona, California" record cited by Stahnke (1961:206) was later cited by Gertsch and Soleglad (1966:25) as occurring in Imperial County, California. Trona is in the extreme northwestern corner of San Bernardino County, a region southwest of, but geographically associated with, the known range of *P. v. vachoni*. This record is here tentatively referred to the nominate subspecies.

Specimens examined.—U.S.A.: CALIFORNIA; *Inyo County*, Saline Valley and Inyo Mts., 1959-1960 (B. Banta), 43 males, 38 females (CAS, AMNH), Death Valley National Monument, Scotty's Ranch (3000 ft.), 13 April 1968 (G. Lytle et al.), 8 males, 17 females (CAS), Ubehebe Crater (2500 ft.), 10 April 1968 (S. C. Williams et al.), 1 male, 5 females (CAS), Grapevine Spring (2100 ft.), 12 April 1968 (S. C. Williams et al.), 8 males, 10 females (CAS), Stovepipe Wells (seal level), 9 April 1968 (S. C. Williams, V. Lee), 1 female (CAS), 2 mi. N Bennett's Well, 15 April 1968 (G. Lytle et al.), 1 male, 2 females (CAS), Travertine Springs, 1/2 mi. E Furnace Creek Inn, 11 April 1968 (S. C. Williams et al.), 6 males, 5 females (CAS), Midway Well (-100 ft.), 11 April 1968 (S. C. Williams et al.), 4 females (CAS), Midway Well, 11 April 1968 (J. Bigelow et al.), 1 female (CAS), Twenty Mule Team Canyon, 14 April 1968 (J. Bigelow, M. A. Cazier), 5 males, 15 females (CAS); *San Bernardino County*, 1/2 mi. E. Saratoga Springs, 10 April 1968 (G. Lytle, J. Bigelow), 1 male, 2 females (CAS), Sheep Creek Springs, 14 May 1971 (R. M. Haradon, R. Leutcke), 1 male, 1 female (CAS); NEVADA; *Clark County*, Tulle Springs, near Charleston Mts., 12 July 1966 (T. Coss), 1 Female (CAS).

Table 1.—Statistical summary of primary denticle counts in rows 1-5 on the pedipalp fixed and movable fingers of *P. vachoni vachoni* and *P. vachoni immanis*. Data include: mean $\pm$ one standard deviation above, sample size (range) below.

Row	Fixed Finger		Movable Finger	
	<i>vachoni</i>	<i>immanis</i>	<i>vachoni</i>	<i>immanis</i>
1	5.64 $\pm$ 0.63 151(4-8)	7.07 $\pm$ 0.95 87(4-9)	7.81 $\pm$ 0.73 108(6-10)	8.78 $\pm$ 0.95 64(5-11)
2	7.26 $\pm$ 0.71 151(5-9)	8.25 $\pm$ 0.72 87(7-10)	9.94 $\pm$ 0.81 108(8-12)	11.45 $\pm$ 0.87 64(9-13)
3	9.01 $\pm$ 0.85 151(7-11)	11.17 $\pm$ 0.94 87(9-14)	11.60 $\pm$ 1.06 108(9-14)	13.33 $\pm$ 2.02 64(10-16)
4	9.68 $\pm$ 0.80 151(7-12)	11.00 $\pm$ 1.15 86(9-15)	11.97 $\pm$ 0.98 108(10-15)	13.36 $\pm$ 1.15 64(11-16)
5	11.54 $\pm$ 1.09 150(9-14)	12.56 $\pm$ 1.27 85(10-15)	18.57 $\pm$ 1.48 108(15-22)	19.05 $\pm$ 1.97 64(15-23)

Paruroctonus vachoni immanis Soleglad, new combination

Fig. 15

Vejovis (Paruroctonus) vachoni: Gertsch and Allred 1965:9 (in part ?); Gertsch and Soleglad 1966:6 (key), 23-265, figs. 14, 15, 22, 49-51, 64, 66, tbl. 3 (in part); Williams 1970b:277, 281 (in part). *Paruroctonus vachoni*: Williams 1972:3 (in part), 1976:2 (in part); Soleglad 1972:72 (key), 75 (in part), 1973:355, tbl. 2 (in part); Haradon 1974:26; Stahnke 1974:138, tbl. 4 (in part). *Paruroctonus immanis* Soleglad 1972:73 (key), 75-82, figs. 1, 3, 4, 6, 8-10, 11-13, tbl. 1, 1973:355, tbl. 2.

Types.—*Paruroctonus immanis*: Holotype male and allotype from U.S.A., California, Riverside County, Indio Hills, 2 miles NW Thousand Palms, 1.2 miles N intersection Varner and Rio del Sol Roads, 17 October 1970 (C. S. and M. E. Soleglad, J. and J. L. Springer). Depository: AMNH. Type locality restricted (M. E. Soleglad, pers. comm. 25 June 1981) from: "two miles west of Thousand Palms."

Diagnosis.—Primary denticle counts in rows 1-5 closer to 7/8/11/11/13 (not 6/7/9/10/12) on fixed pedipalp finger, and 9/11/13/13/19 (not 8/10/12/12/19) on movable pedipalp finger (Table 1); from central San Bernardino County southward in California.

Variation.—Fuscosity variable, ranging from extensive dark markings present to lacking all but vestigial markings on the carapace and tergites. The pale phase occurs with the dark phase along the border of the Coachella Valley and Imperial Valley, is apparently dominant only in the Coachella Valley area, and is unknown from the Mojave Desert. Adult carapace length, males 7.5-9.0 mm, females 7.7-10.4 mm. Pectinal tooth counts are given in Table 2. Fixed finger length/distance *ib* trichobothrium to finger tip, adult males 1.29 ± 0.03 , $n = 8$; females 1.29 ± 0.06 , $n = 14$.

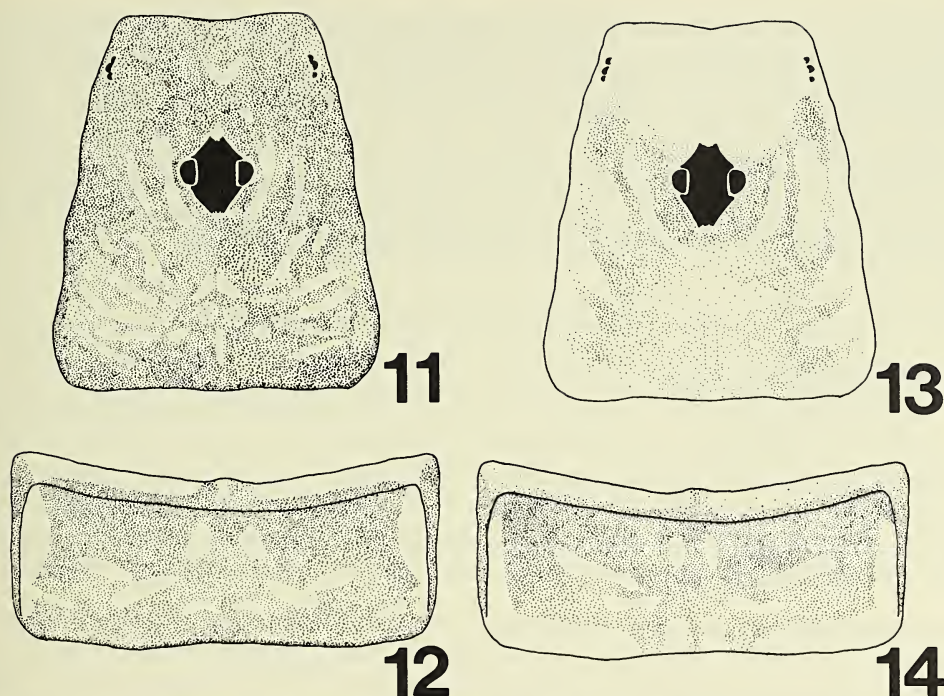
Distribution.—(Fig. 15). Rocky canyons and slopes, central Mojave Desert southward, remaining on northeast side of the Coachella Valley and eastern side of the Imperial Valley, but west of the Colorado River, to U.S.A.-Mexico border.

Remarks.—The *P. immanis* type locality is restricted because the original description placed the locality in what is essentially a sand dune habitat, a habitat in which *P. vachoni* does not occur.

Soleglad (1972) described *P. immanis* from a single locality in the Coachella Valley, California, distinguishing that species from *P. vachoni* by the former essentially lacking dorsal fuscous markings and having a slenderer telson. In addition to specimens from the Coachella Valley area, I have examined several pale specimens intermediate to the *immanis* and typical pigmentation phases from a population near Glamis (Imperial County), a population in which most specimens bear distinct fuscous. Two relatively pale specimens from Salton Sea (Imperial County) were also examined. All the pale specimens I have seen have had at least vestigial fuscous around the median ocular tubercle. Although often very faint, traces of underlying fuscous usually could be seen

Table 2.—Distribution of pectinal tooth counts in *P. vachoni vachoni* and *P. vachoni immanis*.

males	29	30	31	32	33	34	35	36	37
<i>vachoni</i>		1	4	6	14	13	11	4	1
<i>immanis</i>	2	4	10	10	16	8	2	1	
females	20	21	22	23	24	25	26	27	
<i>vachoni</i>		2		24	39	49	19	2	
<i>immanis</i>	1	2	6	15	29	16	1	1	



Figs. 11-14.—Representative dorsal fuscous patterns: 11, *P. vachoni*, carapace; 12, *P. vachoni*, fifth tergite; 13, *P. grandis*, carapace; 14, *P. grandis*, fifth tergite.

on at least some of the tergites. Fuscosity, particularly within the interocular triangle, is more evident in immatures and juveniles than in adults.

There appears to be among some scorpion species a sensitive genetic responsiveness to local substrate shades, resulting in correspondingly lighter or darker dorsal patterns. This correlation has been observed in various species, notably *P. grandis* (Williams 1970b:281, 1980:36; pers. obs.). Considerable variation within a single population has also been observed. Although differences in fuscous patterns or designs can be taxonomically useful, as between *P. vachoni* and *P. grandis*, or between *Paruroctonus boreus* (Girard) and *Paruroctonus silvestrii* (Borelli), variation in the intensity of a basic pattern does not appear to be significant at the species or subspecies level. Because the Coachella Valley area appears to provide a generally lighter substrate than is typical of other areas inhabited by *P. vachoni*, I consider the Coachella Valley *immanis* population to be simply an edaphic variant within the subspecies *P. v. immanis* as defined herein.

The ratio, telson depth/metasomal segment V width, reveals no sexual dimorphism among adult *P. vachoni* ($t = 0.98$, $P > 0.05$, $n = 60$), nor any significant difference between *P. v. vachoni* and *P. v. immanis* ($t = 1.92$, $P > 0.05$, $n = 60$). The *P. immanis* type population falls well within the range of variation for this ratio reported for *P. vachoni* above. In immatures and juveniles the telson depth is always much less than the width of segment V.

Specimens examined.—U.S.A.: CALIFORNIA; *San Bernardino County*, approx. 26 mi. E. Yermo, 16 April 1965 (V. Lee), 1 male (CAS), 3 mi. W Amboy, 11 May 1968 (Foster, M. A. Cazier), 1 male (CAS), 3 mi. W Amboy, 11 May 1968 (Foster, M. A. Cazier), 1 male (CAS), 3 mi. W Amboy, 17 May 1968 (J. Bigelow et al.), 2 females (CAS), approx. 25 mi. E Twentynine Palms, 6 May 1972 (R. M. Haradon, J. L. Marks), 2 males, 4 females (CAS), approx. 27 mi. E Twentynine Palms, 2 September 1972 (R. M. Haradon, J. L. Marks), 2 males (CAS); *Riverside County*, Indio Hills, 2 mi. NW Thousand Palms, 17 October 1970 (M. E. Soleglad et al.), male holotype, allotype (AMNH), approx. 20 mi. E North Palm Springs along Dillon Rd., 13 May 1972 (R. M. Haradon), 1 male (CAS), Little San Bernar-

dino Mts., Berdoo Canyon, 2.7 mi. NE jct. Dillon Rd., 6 May 1972 (R. M. Haradon), 1 male, 5 females (CAS), 3.4 mi. NE jct. Dillon Rd., 9 April 1972 (R. M. Haradon, J. L. Marks), 1 female (CAS), 2.4 $\pm$ 0.1 mi. NE jct. Dillon Rd., 1 April 1972 (R. M. Haradon, J. L. Marks), 2 males, 3 females (CAS); *Imperial County*, Salton Sea, 26 December 1964 (V. Roth), 1 male, 1 female (AMNH), 11 mi. NE Glamis, 28 October 1967 (M. A. Cazier et al.), 1 male, 1 female (CAS), 10 mi. NE Glamis (approx. 200 ft.), 28 October 1967 (M. A. Cazier et al.), 5 males, 6 females (CAS), 9 mi. NE Glamis, 28 October 1967 (M. A. Cazier et al.), 6 males, 12 females (CAS), 9 mi. NE Glamis, 14 October 1967 (M. A. Cazier), 2 males, 2 females (CAS), Chocolate Mts., N inspection station, 24 December 1959 (V. Roth), 1 female (AMNH), 3 mi. N Winterhaven, 2 April 1960 (V. Roth), 1 male (AMNH).

Paruroctonus vachoni, intermediate populations

Distribution.—See Figure 15.

Remarks.—Samples of *P. vachoni* from along the Colorado River in Arizona were generally morphologically intermediate to *P. v. vachoni* and *P. v. immanis*, but were more similar to the former in the primary denticle counts on the pedipalp fingers (mean denticle counts on fixed finger 7/8/10/10/11, on movable finger 8/10/12/12/18). The subspecies dentition formulas given above permitted 83% separation of the *P. v. immanis* and Arizona samples. The mean pectinal tooth counts of males was relatively low (32.2

subspecies dentition formulas given above permitted 83% separation of the *P. v. immanis* and Arizona samples. The mean pectinal tooth counts of males was relatively low (32.2 ± 1.62 , $n = 56$), but moderately high among females (24.5 ± 1.15 , $n = 146$). The ratio, fixed pedipalp finger length/distance *ib* trichobothrium to finger tip, among adults was similar to that of *P. v. immanis* (one male 1.32, females 1.27 ± 0.04 , $n = 32$). The adult size of the Arizona scorpions was similar to *P. v. immanis* (carapace length of one male 7.8 mm, 32 females 7.8–10.3 mm). All the Arizona specimens were very darkly pigmented. In addition to the Arizona specimens, two *P. vachoni* specimens from California, near the Colorado River, were also morphologically intermediate to the two subspecies.

Specimens examined.—U.S.A.: ARIZONA; *Mohave County*, Lake Mead Natl. Recreation Area, Willow Beach, 29 August 1965 (V. Lee), 1 male (CAS), Willow Beach, 18 October 1971 (Foster and Cazier), 1 male, 4 females (OFF), Topock, no other data, 1 female (OFF); *Yuma County*, "P" (= Black) Mt., 6 mi. E Parker, 5 April 1969 (Cazier et al.), 14 males, 27 females (OFF), 14 March 1976 (M. A. Cazier, O. F. Francke), 5 females (OFF), 2 mi. N Parker, 1 October 1970 (F. Ennik), 1 female (CAS), Trigo Mts., 15 mi. S Cibola Lake Rd., 3–4 April 1969 (Cazier et al.), 10 males, 33 females (OFF), 1/4 mi. N McPaul Bridge, near Gila River, 24 October 1973 (M. Kolner, R. Garrison), 1 male, 2 females (OFF); CALIFORNIA; *San Bernardino County*, 1 mi. N Earp on U.S. 520, 31 October 1970 (F. Ennik et al.), 3 males, 1 female (CAS); *Riverside County*, Mule Mts. Coon Hollow, 9 November 1961 (D. Richman), 1 female (AMNH).

Paruroctonus mesaensis Stahnke

Figs. 1, 9, 10, 17, 19

Paruroctonus mesaensis Stahnke 1957:253–259, 1961:206, 207, tbl. 1, 1965:262, 1974:138; Gertsch 1958:15–17 (erratum p. 17, "*imperialis*"), tbl. 5; Williams 1972:3, 1976:2, 1980:32 (key), 37–38, figs. 37D, 39, 44 (in part, misidentification); Sologlad 1972:72 (key), 75, 1973:355, tbl. 2, fig. 7; Tourtlotte 1974:178; Bowerman 1976:363; Brownell 1977:479; Hadley and Jackson 1977:85; Wright et al. 1977:197, 203; Polis and Farley 1979a:33, 1979b:517, 1980:620.

Vejovis (Paruroctonus) mesaensis: Gertsch and Allred 1965:9; Gertsch and Sologlad 1966:6 (key), 35–37, 39, 40, figs. 26, 42–45, 55, 61, 62, 67, 70, tbl. 5; Williams and Hadley 1967:106 (key), 113–114; Hadley and Williams 1968:727; Williams 1968b:313, 1969:291, 1970b:277, 281; Newlands 1972:248.

Vaejovis mesaensis: Diaz-Nájera 1975:7, 10, 31.

Types.—*Paruroctonus mesaensis*: Holotype female from U.S.A., Arizona, Maricopa County, city dump NW Mesa, 13 March 1947 (F. Parrat, I. F. Nichols). Allotype from same locality, 14 September 1939 (H. L. Stahnke). Depository: H. L. Stahnke collection, Tempe, Arizona.

Diagnosis.—A species of subgenus *Smeringurus*; adult males with weakly scalloped pedipalp fingers, closed fingers form at most a narrow proximal gap (Fig. 10); legs 1 and 2 lacking large bristle at mid-length of basitarsus along inferior retrolateral row of spinules (Fig. 19); nine or more very long retrolateral setae in an even row on basitarsus of third pair of legs (Fig. 17); 10 to 14 pairs of ventrolateral setae on metasomal segment V; fuscosity usually entirely lacking (when present, markings are few and extremely weak); pedipalp fingers light yellow, not darker than light yellow palm; ventral carinae on metasomal segments I-III obsolete or smooth; telson depth/metasomal segment V width, less than 0.96.

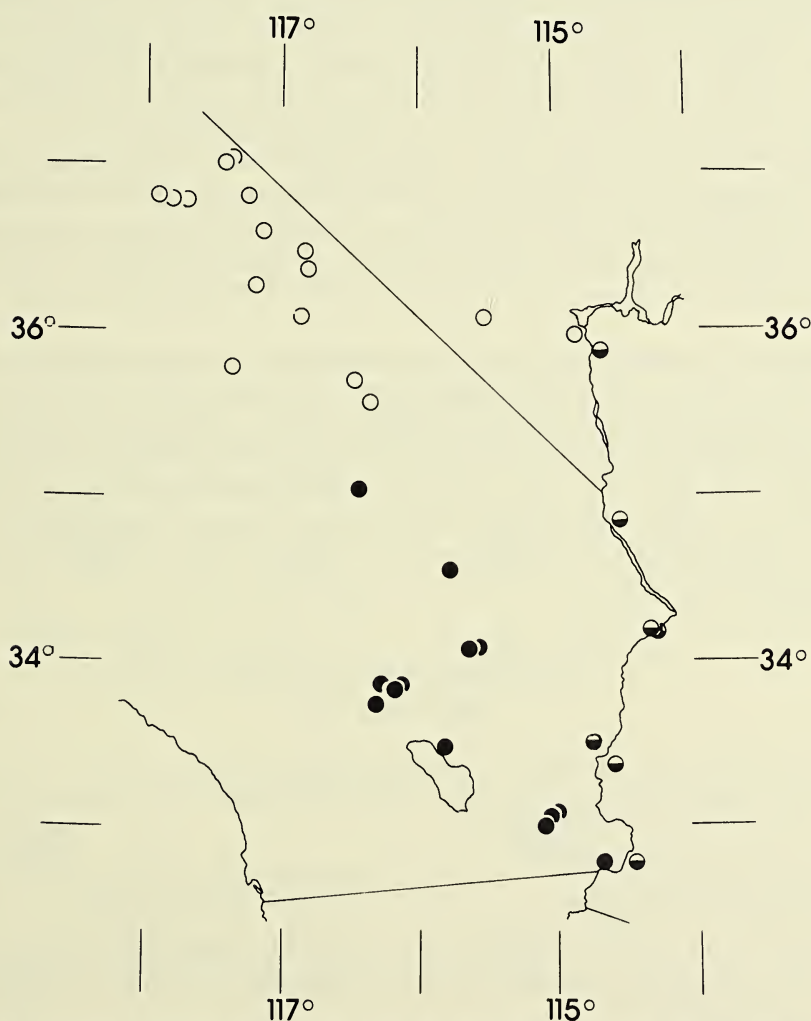


Fig. 15.—Southern California and adjacent areas, showing distribution of *P. vachoni vachoni* (white circles), *P. vachoni immanis* (black circles), and *P. vachoni vachoni* X *immanis* (white and black circles).

Variation.—The scalloping and the resulting proximal gap on the pedipalp fingers varied among adult males from that shown in Figure 10 to that shown for *P. aridus* in Figure 8, and among adult females from what is shown in Figure 9 to a slightly more scalloped state. The anterior margin of the carapace in most specimens was concave, but in some specimens was essentially straight or slightly convex. The number of primary denticles in row 6 on the fixed pedipalp finger in adult males varied from 11 to 20, and thus overlaps the ranges of the other three species in the subgenus. Of the four species in *Smeringurus*, *P. mesaensis* is the most widely distributed and the most morphologically variable. Eight relatively distinct populations were identified, all of which differed significantly from one another in one or more of the following characters: Adult size, mean number of pectinal teeth, morphometric ratios, numbers of primary denticles on the pedipalp fingers, and number and development of the carinal setae on the metasoma. Specimens from Saratoga Springs (San Bernardino Co.) in California had faint fuscous markings on the carapace and tergites. A few specimens from near Borrego Springs (San Diego Co.) in California also had faint fuscous markings on the carapace, and yellowish-orange pedipalps, carapace, and mesosoma, which contrasted with the typically pale yellow metasoma. All other samples of *P. mesaensis* from the Borrego Desert that I have studied have been uniformly pale yellow, and entirely lacked fuscosity.

Distribution.—Open desert areas, primarily eolian sand; in California, from Inyo County (Stovepipe Wells), southward throughout the Mojave and Colorado Deserts; in Arizona, from Maricopa County (Phoenix area) southwest to Yuma County, and along the Colorado River north into Mohave County; in Mexico, northeastern coast of Baja California Norte, south to near Puertecitos, and northwestern Sonora, south to Cabo Lobos.

Remarks.—Geographic variation in *P. mesaensis* has become the subject of a separate study. The above account is based upon samples from the several thousand specimens of *P. mesaensis* in the collection of the California Academy of Sciences, representing more than 120 localities throughout the range stated. The record (Williams 1980:38) of *P. mesaensis* from Bahia San Luis Gonzaga, Baja California Norte (CIS), has now been identified as *P. grandis*. Questionable records include: Jaraguay Summit, Baja California Norte, Mexico (Williams 1980:38), and Isla Tiburon, Sonora, Mexico (Gertsch and Soleglad 1966:40).

Paruroctonus grandis (Williams)

Figs. 5, 6, 13, 14

Vejovis (*Paruroctonus*) *grandis* Williams 1970b:277-281, figs. 1-2, tbl. 1.

Paruroctonus grandis: Williams 1972:3, 1980:32 (key), 35-36, figs. 39, 42; Soleglad 1972:72 (key), 75, 1973:355, tbl. 2; Stahnke 1974:138.

Vaejovis grandis: Diaz-Nájera 1975:6, 9.

Paruroctonus mesaensis: Williams 1980:38 (in part, misidentification, from Bahia San Luis Gonzaga, Baja California Norte, Mexico).

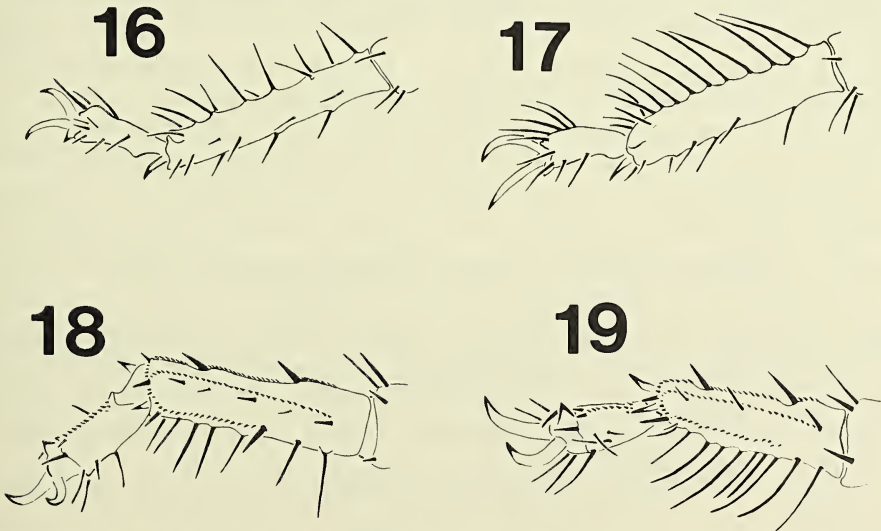
Types.—*Vejovis grandis*: Holotype male and allotype from Mexico, Baja California Norte, Oakies Landing, 27 mi. S Puertecitos, 12 June 1968 (S. C. Williams et al.). Depository: CAS, Type No. 10417.

Diagnosis.—A species of subgenus *Smeringurus*; adult males with moderately scalloped pedipalp fingers, closed fingers form distinct proximal gap (Fig. 6), 15 or fewer primary denticles in row 6 of fixed finger; legs 1 and 2 with large bristle at mid-length of basitar-

sus along inferior retrolateral row of spinules (similar to Fig. 18); eight or fewer irregularly positioned retrolateral setae on basitarsus of third pair of legs (similar to Fig. 16); eight pairs of ventrolateral setae on metasomal segment V; dorsal setae on metasomal segment II absent or distinctly smaller than dorsal setae on segments III-IV; fuscous markings usually distinct and extensive, but do not extend into interocular triangle (Fig. 13) or to the lateroposterior margin of tergites 3-6 (Fig. 14); juveniles and adults with light to dark reddish or reddish-brown pedipalp fingers, fingers darker than light yellowish palm; chela length/width, less than 2.96 in adult males; telson depth/metasomal segment V width, in adults equal to or less than 0.96; fixed finger length/distance *ib* trichobothrium to finger tip, in adults equal to or less than 1.22.

Variation.—The scalloping and resulting gap on the pedipalp fingers varied among adult males from slightly more to slightly less than the state shown in Figure 6, and among adult females from what is shown in Figure 5 to a slightly more scalloped state; fingers were essentially unscalloped on immatures and juveniles. The primary denticles in row 6 on the fixed pedipalp finger in adult males varied from 4 to 18; counting only the larger contiguous denticles of similar size, the count seldom exceeded 12. At least vestigial fuscous markings were always present on the carapace and tergites. Fuscousness was most distinct in juveniles and immatures. In the paratopotypic sample: Chela length/width, in adult males 2.78 ± 0.14 , $n = 40$, in adult females 2.86 ± 0.14 , $n = 46$; telson depth/metasomal segment V width, in adults 0.89 ± 0.05 , $n = 83$; fixed finger length/distance *ib* trichobothrium to finger tip, adults 1.17 ± 0.03 , $n = 85$. Samples representing other populations fell within these ranges of variation, with the exception of adult insular samples having the chela length/width in males 2.50 ± 0.03 , $n = 3$, and in females 2.64 ± 0.10 , $n = 6$.

In all peninsular samples the metasomal setae were well developed, but in the coastal samples from Puertecitos to Bahia San Luis Gonzaga the dorsal setae, particularly in males, were very long, slender, and more hairlike than bristly. In these samples the telson setae were also proportionately longer and slenderer, and occasional specimens had nine retrolateral setae on the basitarsus of leg 3.



Figs. 16-19.—Apotele and tarsal leg segments: 16, *P. vachoni*, right third leg, dorsal aspect; 17, *P. mesaensis*, right third leg, dorsal aspect; 18, *P. vachoni*, right first leg, ventral aspect; 19, *P. mesaensis*, right first leg, ventral aspect.

The insular populations differed from those on the peninsula in having very short dorsal metasomal setae on adults. The adult size attained on the islands is apparently greater than that of any known peninsular population. Carapace lengths on the peninsula varied among males 6.5-8.1 mm, and among females 7.5-9.6 mm (but usually less than 9.0 mm); on the islands males varied 8.5-9.1 mm, and females varied 9.6-11.0 mm. One female from Isla Angel de la Guarda with a carapace 7.8 mm long did not appear mature. Although gigantism has been reported for Gulf of California island populations among other Baja California scorpion species (Williams 1980:121), the relatively large size of the insular *P. grandis* specimens is not unusual for the subgenus, being comparable to certain populations of *P. vachoni*. In large insular adults the depth of the concavity of the anterior margin of the carapace was greater than what was observed among peninsular specimens. Several morphometric ratios among adults differed significantly ($P < 0.05$) between the insular and peninsular samples, reflecting positions along an apparently common, rather than a divergent, ontogenetic regression line. The morphometric differences observed did not provide a practical separation of these populations, and were of questionable significance, given the small island samples. Three specimens out of 44 from the islands bore a fuscous pattern similar to that of *P. vachoni*.

Distribution.—Rocky desert habitats in northeastern Baja California, Mexico, from near the U.S.A.-Mexico border south to Punta Trinidad, Baja California Sur, and from Isla Mejia, Isla Angel de la Guarda, and Isla Estanque in the Gulf of California.

Remarks.—The above account is based upon the samples of more than 1500 specimens reported by Williams (1970b:280-281, 1980:36).

Paruroctonus aridus Soleglad

Figs. 7, 8

Paruroctonus aridus Soleglad 1972:72 (key), 82-86, figs. 2, 5, 7, 9, tbl. 1, 1973:355, tbl. 2; Williams 1976:2.

Types.—*Paruroctonus aridus*: Holotype male from U.S.A., California, San Diego County, Anza-Borrego Desert State Park, 1 mile W Seventeen Palms Oasis, 24 October 1970 (C. S. and M. E. Soleglad, J. and J. L. Springer). Allotype from same locality, 12 June 1971 (M. E. Soleglad, L. R. Erickson). Depository: AMNH.

Diagnosis.—A species of subgenus *Smeringurus*; adult males with weakly scalloped pedipalp fingers, closed fingers form at most a narrow proximal gap (Fig. 8), 18 or more primary denticles in row 6 of fixed finger; legs 1 and 2 with large bristle at mid-length of basitarsus along inferior retrolateral row of spinules (similar to Fig. 18); eight or fewer irregularly positioned retrolateral setae on basitarsus of third pair of legs (similar to Fig. 16); eight pairs of ventrolateral setae on metasomal segment V; dorsal setae on metasomal segment II about as long as dorsal setae on segments III-IV; fuscosity essentially limited to faint interocular crescent; juveniles and adults with light to dark reddish or reddish-brown pedipalp fingers, fingers darker than pale yellow palm; chela length/width, adult males greater than 2.95; fixed finger length/distance *ib* trichobothrium to finger tip, adults equal to or greater than 1.23.

Variation.—The scalloping and resulting proximal gap on the pedipalp fingers varied among adult males from what is shown in Figure 8 to that shown for *P. mesaensis* in Figure 10; adult females were as shown in Figure 7. The primary denticle counts in row 6 of the pedipalp fixed finger among adult males varied from 20 to 26; the lower limit given

in the diagnosis above is a statistical estimate based upon a small sample ($n = 12$). One immature male, in which the full complement of primary denticles presumably had not yet developed, had counts of 14 and 16. The same immature specimen showed slightly more fuscosity around the median eyes and posterior region of the carapace. Chela length/width, adult males 3.22 ± 0.14 , $n = 6$; two adult females, 2.83 and 3.16. Fixed finger length/distance *ib* trichobothrium to finger tip, adult males 1.28 ± 0.03 , $n = 6$; two adult females, 1.27 and 1.33. The development of the ventral metasomal carinae I-III was intermediate to that of *P. mesaensis* (smooth) and *P. grandis* (usually weakly granular), making any distinction between taxa very subjective. The anterior margin of the carapace tended to be slightly convex in young adult and earlier instars. This margin in older adults was essentially straight but with a subtle medial concavity.

Distribution.—Known only from the type locality, where it inhabits rocky, sedimentary soil.

Remarks.—Two characters used by Soleglad (1972:82) to separate *P. aridus* from *P. immanis* (= *P. vachoni immanis*) were found, among additional specimens, to be no longer useful. The numbers of pectinal teeth in *P. aridus* males (33-40) and females (25-27) essentially coincide with the ranges in *P. vachoni* (Table 2). A similar range in numbers of pectinal teeth is shared by all the species in the subgenus. Tendencies toward higher or lower counts within this range appear to vary among populations within each species. On the holotype male of *P. aridus* I counted 34/32 pectinal teeth, not 36/36 as reported by Soleglad (1972:tbl. 1).

The ratio, telson depth/metasomal segment V width, is quite variable in both *P. aridus* and *P. vachoni*. Among adults I found no significant difference ($P > 0.05$) between the sexes in either species. There was a significant difference between the species ($t = 2.54$, $n = 66$; where *P. aridus* = 0.976 ± 0.073 , $n = 6$, and *P. vachoni* = 1.050 ± 0.068 , $n = 60$), but the respective ranges in variation do not permit a practical separation.

The convex anterior carapacial margin illustrated by Soleglad (1972:78, fig. 5) appears to be characteristic of young adult and earlier instars of *P. aridus*. Larger and presumably older specimens, including the holotype and allotype, of this species have an essentially straight anterior margin. Rounded anterior-lateral margins also occur in large specimens of *P. grandis*.

Specimens examined.—U.S.A.: CALIFORNIA: *San Diego County*, Anza-Borrego Desert State Park, 1 mi. W Seventeen Palms Oasis, 24 October 1970 (M. E. Soleglad et al.), holotype male (AMNH), 12 June 1971 (M. E. Soleglad, L. R. Erickson), allotype (AMNH), 10 August 1974 (R. M. Haradon, W. E. Savary), 6 males, 2 females (CAS).

KEY TO SUBGENERA OF *PARUROCTONUS* WERNER

- 1. Numerous intercarinal setae on ventral surface of metasomal segments I-IV present (Fig. 1); in adults and juveniles, metasomal segment III length/width greater than 1.90 *Smeringurus*, new subgenus
- Numerous intercarinal setae on ventral surface of metasomal segments I-IV absent; in adults and juveniles, metasomal segment III length/width less than 1.90. *Paruroctonus*

KEY TO SPECIES AND SUBSPECIES OF SUBGENUS *SMERINGURUS*

1. Basitarsus on legs 1 and 2 lacking large bristle along inferior retrolateral row of spinules (Fig. 19); 10 or more pairs of ventrolateral setae on metasomal segment V *mesaensis* Stahnke
 Basitarsus on legs 1 and 2 bearing large bristle along inferior retrolateral row of spinules (Fig. 18); eight or fewer pairs of ventrolateral setae on metasomal segment V . . . 2
2. Closed pedipalp fingers of adult male form at most a narrow proximal gap (Fig. 8), with 18 or more primary denticles in row 6 of fixed finger; fuscosity limited to vestigial interocular crescent *aridus* Soleglad
 Closed pedipalp fingers of adult male form conspicuous proximal gap (Figs. 4, 6), with 15 or fewer primary denticles in row 6 of fixed finger; fuscosity extensive on carapace and tergites (Figs. 11-14) 3
3. Closed pedipalp fingers of adult male form moderate gap (Fig. 6); fuscosity essentially lacking in interocular triangle (Fig. 13), and does not extend to lateroposterior margin on tergites 3-6 (Fig. 14); paired dorsal metasomal setae on segment II absent or much smaller than dorsal setae III-IV. *grandis* (Williams)
 Closed pedipalp fingers of adult male form prominent gap (Fig. 4); fuscosity extends into most or all of interocular triangle (Fig. 11), and to lateroposterior margin on tergites 3-6 (Fig. 12); paired dorsal metasomal setae on segment II about as long as setae III-IV. 4
4. Primary denticle counts in rows 1-5 on pedipalp fingers close to 6/7/9/10/12 on fixed finger, 8/10/12/12/19 on movable finger; from Death Valley region in California and southwestern Nevada (Fig. 15). *vachoni vachoni* Stahnke
 Primary denticle counts in rows 1-5 on pedipalp fingers close to 7/8/11/11/13 on fixed finger, 9/11/13/13/19 on movable finger; from southern Mojave and Colorado Deserts in California (Fig. 15). *vachoni immanis* Soleglad

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PREY OF TWO SYNTOPIC SPIDERS WITH DIFFERENT WEB STRUCTURES

David H. Wise and José L. Barata¹

Department of Biological Sciences
University of Maryland Baltimore County (UMBC)
Catonsville, Maryland 21228

ABSTRACT

In order to determine the extent to which differences in web structure are correlated with divergence in diet, we collected and identified prey from the webs of two syntopic orb-weavers whose webs differ markedly in architecture. The species studied were the basilica spider *Mecynogea lemniscata*, and the labyrinth spider *Metepeira labyrinthea*. Two nearby allotopic populations were also compared. We determined the size and taxonomic category of the prey of both species, web height, and the type of vegetation supporting the web.

The diets of syntopic populations were very similar. No statistically significant differences were found between syntopic *Mecynogea* and *Metepeira* in either the types or size of prey collected from the webs. Allotopic populations differed in these aspects of the diet, but the overlap was substantial. *Metepeira* usually placed its web higher and on less rigid vegetation than did *Mecynogea*. However, the overlap was extensive, particularly when the species occurred together. Syntopic basilica and labyrinth spiders were significantly more similar than allotopic populations in where they placed the web.

Several authors have suggested that exploitative competition for prey between syntopic spiders has led to the evolution of differences in web structure as a means of competitive coexistence. The results of this study make it difficult to argue that avoidance of competition for food is the primary reason syntopic species have evolved different web structures.

INTRODUCTION

The type of web a spider spins is a component of its foraging behavior. Web design is a potentially important niche parameter if it influences a spider's diet, since species differences in web structure may lessen overlap in prey utilization and contribute to reduced interspecific competition. The argument that different types of spider webs have evolved in response to exploitative competition for prey rests upon the assumption, among others, that the structure of the web substantially influences the kinds of prey captured by its owner. The extent to which structural differences correlate with differences in diet is most directly approached by examining the prey of syntopic species that resemble each other in phenology and body size but differ in web architecture.

The basilica spider *Mecynogea lemniscata* (Walckenaer), and the labyrinth spider *Metepeira labyrinthea* (Hentz), are such species. They are syntopic in forested areas of central Maryland, USA, to the extent that on occasion a spider may construct its web within a few cm of the other species. Individuals of both species often remain at the same

¹ Present address: Maryland Science Center, 601 Light St., Baltimore, MD 21230

web site for several weeks. In Maryland these species mature during July and August, and females can live through October. Basilica spider females are larger at maturity than labyrinth spiders, though the difference is not substantial. Mean carapace widths ($\pm$ s.e.) in a 1978 sample of *Mecynogea* and *Metepeira* were 2.16 ± 0.03 mm and 2.01 ± 0.04 mm, respectively (pers. obs.). Both species belong to the orb-weaving family Araneidae, but they spin dissimilar webs. The labyrinth spider constructs a typical vertically oriented orb with a viscid catching spiral. An irregular barrier web houses a retreat. *Mecynogea*'s web is much different and resembles a linyphiid snare. The basilica spider spins a horizontal orb that is modified into a dome under which the spider waits for prey. *Mecynogea*'s orb differs further from that of most other araneids in being non-viscid (Levi 1978). Orbs of adult female labyrinth and basilica spiders differ markedly in mesh size. Strands of the labyrinth spider's catching spiral form a series of variable rectangles, approximately 2 x 5 mm on average. Distances between the silk of the basilica spider's orb are smaller, about 1 mm or less. Thus openings in *Metepeira*'s web are approximately 10X larger than those of *Mecynogea*'s snare. We determined whether these substantial differences in web shape and mesh size are correlated with a divergence in diet.

STUDY AREAS AND METHODS

The research was conducted in three areas on the Patuxent Wildlife Research Center in Prince Georges County, Maryland, USA: two in which one species was rare (designated the allotopic *Mecynogea* and allotopic *Metepeira* areas) and a third, the syntopic area, where both species were abundant. We selected allotopic areas in addition to a site where both co-occurred because 1) a comparison of dietary differences in syntopy with the extent of divergence in diet between populations that inhabit different areas would provide information on the extent to which their diets might reflect spatial variation in the size and taxa of available prey, and 2) we wanted to examine the alternative possibility that diets diverge in syntopy due to differences in web placement, possibly resulting from interspecific competition. The allotopic *Mecynogea* area was a narrow 100-m zone of shrubs and young pine bordering both sides of a dirt road adjacent to a marsh. The allotopic *Metepeira* area was a 70 x 120 m portion of a lake-side oak-beech forest. Forest margin and marsh-side shrubs composed the syntopic area. It was discontinuous, with one sub-area beside a marsh, and another extending from either side of a dirt road between a pond and an open field. These sub-areas were 100 m apart and supported approximately equal numbers of both species.

All three areas were censused in July 1978 and the site of every web with a female spider was marked with a numbered tag. In the two allotopic areas 72 *Mecynogea* and 89 *Metepeira* were located. We tagged 66 *Mecynogea* and 55 *Metepeira* web sites in the syntopic area. Females were studied since mature males wander and do not live as long as females.

Prey upon which spiders were feeding and insect exoskeletons left in the web were collected from occupied webs July through September. Each web was visited two to five times a day between 0700 and 1600. On a few occasions prey was collected later in the day, up to 2300 h. At the start of the study each web was visited on alternate days, but the decreased number of spiders later in the season made it possible to visit each occupied web several times a day. Collected prey was preserved in 70% ethanol and later identified to order, and to family whenever possible, using the keys of Jaques (1947), Borror and Delong (1964), and Borror and White (1970). We calculated a prey-size index equal to the product of the length and the square of the width.

Table 1.—Identity of prey collected from webs in two allotopic areas and the single syntopic area. Major families are distinguished for the more frequently represented orders.

	Allotopic Areas		Syntopic Area	
	<i>Mecynogea</i>	<i>Metepeira</i>	<i>Mecynogea</i>	<i>Metepeira</i>
Coleoptera				
Chrysomelidae	29	1	11	18
Curculionidae	3	47	2	10
Cantharidae	10	3	6	4
Scarabaeidae	0	3	0	3
Scolytidae	0	4	1	2
Staphylinidae	1	2	1	1
Other Families	5	2	3	1
Unidentified Family	0	19	2	4
Total Coleoptera	48	81	26	43
Hymenoptera				
Formicidae	37	18	16	11
Ichneumonidae	1	7	4	6
Sierolomorphidae	0	2	3	0
Pompilidae	0	4	0	2
Halictidae	0	2	0	4
Braconidae	2	2	0	0
Other Families	2	8	0	1
Unidentified Family	0	15	1	5
Total Hymenoptera	42	58	24	29
Homoptera				
Cicadellidae	9	3	9	7
Flatidae	7	3	9	4
Aphididae	2	1	1	3
Delphacidae	4	0	0	0
Other Families	2	2	3	2
Unidentified Family	2	0	0	0
Total Homoptera	26	9	22	16
Diptera				
Tabanidae	2	2	0	3
Other Families	5	2	4	2
Unidentified Family	4	0	3	3
Total Diptera	11	4	7	8
Odonata	10	5	1	5
Lepidoptera	9	4	5	1
Hemiptera	4	1	3	0
Orthoptera	1	0	1	1
Neuroptera	1	0	0	1
Unidentified Order	8	8	5	7
Unidentified Larvae	2	0	3	1

Our primary goal was to document the extent to which diets of the syntopic populations differed. Since we also wanted to determine whether syntopic populations of *Mecynogea* and *Metepeira* differed more than allotopic populations in where they placed their webs, we also recorded web height and the type of substrate to which the spider attached the supporting silk. Substrates were scored on a subjective scale of rigidity ranging from 1 to 8: live pine (1), live vine (greenbrier, *Smilax*) (2), mixed live and dead vines (3), dead vine (4), live shrub (5), live deciduous twigs (6), mixed live and dead deciduous twigs (7) and dead deciduous twigs (8).

Data were analyzed with the use of UCLA Biomedical Computer Programs [multiway frequency tables (BMDP3F) and analysis of variance (BMDP2V)] and nonparametric techniques (Conover 1971).

RESULTS

Prey Captured.—Coleoptera, Hymenoptera, Homoptera and Diptera were the major insect orders captured by *Mecynogea* and *Metepeira* (Table 1), with beetles and hymenopterans comprising over half of the prey found in the webs of each species. Differences between the diets of allotopic populations were statistically significant, but the diets of *Mecynogea* and *Metepeira* in syntopy did not differ significantly in the relative proportions of these prey orders (Fig. 1). However, the apparently greater similarity in prey captured when the species are syntopic is not statistically significant ($\chi^2 = 5.59$, $p > 0.2$, for the 3-way interaction term in the $2 \times 5 \times 2$ contingency table of spider species $\times$ prey order $\times$ area. The size of the interaction term indicates whether the extent to which the two spiders differ in the relative proportion of prey in the diet is similar for the syntopic and allotopic comparisons).

Diets of the two syntopic spider populations also closely resemble each other in terms of the relative representation of the families of prey (Table 1). At this level of resolution the prey of allotopic populations does appear more different than the prey in syntopy, particularly for the two most numerous families of Coleoptera. Allotopic *Mecynogea* captured many chrysomelids but very few curculionids, whereas allotopic *Metepeira* exhibited the opposite pattern. However, in syntopy these differences between the basilica and labyrinth spiders' diets decreased. When together, both species snared substantial numbers of chrysomelids, and the apparent specialization of *Metepeira* on curculionids disappeared.

Prey of allotopic *Metepeira* tended to be larger than that of the allotopic *Mecynogea* population [Fig. 2; χ^2 (median test) = 5.88, $p = 0.02$]. However, in syntopy the median prey sizes were more similar and did not differ significantly [$\chi^2 = 2.55$, $p = 0.11$]. We tested for differences in prey size with a nonparametric procedure because the data are skewed, though a shortcoming of nonparametric approaches is the lack of convenient procedures to test for interactions between treatments (Conover, 1971). Although large deviations from normality can make an Analysis of Variance (ANOVA) too conservative, the small value of the interaction term in the 2×2 ANOVA of log (prey size) (Table 2) suggests that the greater similarity in prey size in syntopy would also be judged statistically non-significant by an equivalent nonparametric test. Note that the overall effect of species in the ANOVA (p of $F = 0.09$) is in general agreement with the results of the two nonparametric comparisons.

Web Placement.—The heights above the ground at which both species built their webs overlapped, particularly in the syntopic area (Fig. 3). *Metepeira* placed its web significantly higher in the vegetation than did the basilica spider (Table 2). This difference between the species in mean web height was significantly less in syntopy, as indicated by the significant interaction term in the ANOVA.

Both species used similar vegetation for supporting their webs, but they differed in the relative proportions of types of substrate selected. (Fig. 4). The labyrinth spider usually spun its web on more rigid substrate. The difference between syntopic populations was significantly less than for the allotopic comparison (Fig. 4; $\chi^2 = 24.4$, $p < 0.001$, for the 3-way interaction term in the $2 \times 4 \times 2$ contingency table of spider species $\times$ substrate $\times$

Table 2.—Two-way ANOVA of log (prey size) and web height. Treatments are species (*Mecynogea*, *Metepeira*) and area (allotopic, syntopic). A significant interaction term (species x area) indicates that the species are more alike in syntopy than allotopy. A logarithmic transformation of prey size was required to make variances homogeneous and reduce the skewness of the data distribution. No transformation of web height was necessary.

Source	d.f.	M.S.	F	Significance
Log (Prey Size)				
Species (S)	1	0.958	2.81	0.09
Area (A)	1	0.050	0.15	0.70
S x A	1	0.128	0.38	0.54
Error	486	0.341		
Web Height				
Species (S)	1	254.42 x 10 ³	178.92	<0.001
Area (A)	1	0.50 x 10 ³	0.35	0.55
S x A	1	9.24 x 10 ³	6.49	<0.01
Error	200	1.42 x 10 ³		

area. Contiguous classes of substrate scores were pooled in order to yield expected values > 5 for the contingency table analysis).

DISCUSSION

Bristowe (1941) discusses how different snares capture different types of prey as part of his argument that the diversity of spider hunting habits reflects evolution to avoid exploitative competition for food among species occupying the same habitat. Robinson (1981) suggests that in the spider community he studied, specialization on different-sized prey permits coexistence within a guild. Both a spider's size and its web characteristics are important predictors of the size and type of prey the spider will capture (Bristowe 1943, Enders 1975, Chacón and Eberhard 1980, Riechert and Luczak in press). Uetz *et al.* (1978) argue that these aspects of a web-builder's foraging behavior, in particular the spacing of the web's mesh, reflect specialization on different sizes and taxa of prey and hence permit coexistence among competing syntopic species.

Two basic assumptions underlie arguments relating differences in web structure to competitive coexistence: 1) exploitative interspecific competition for food is important in spider communities, and 2) different webs capture different kinds of prey. Although many spiders are food-limited in nature, the few experimental studies of competition that have been conducted so far have not uncovered evidence of major interspecific competition in spider communities (Wise, in press). Absence of significant interspecific competition over ecological time does not rule out its possible role in causing the evolution of differences in prey specialization. However, establishing that competition actually has caused the evolution of niche differences is difficult (Connell 1980); furthermore, other hypotheses can explain why species differ in trophic characters (e.g., Strong 1980). The second assumption, that differences in web structure lead to differences in prey captured, can be tested directly. The results of this study suggest that two species with markedly different webs do not necessarily capture markedly different prey.

Syntopic populations of the basilica and labyrinth spiders exhibited remarkable overlap in diet, especially considering the species differences in mesh size and web morphology. One might expect that the non-sticky sheet web of *Mecynogea* would capture a different array of insect taxa than the sticky, vertically oriented orb of *Metepeira*. On the contrary, the overlap in prey taxa was high. Pianka's (1973) index of niche overlap was 0.96 for the syntopic populations. Although *Mecynogea* is slightly larger than *Metepeira*,

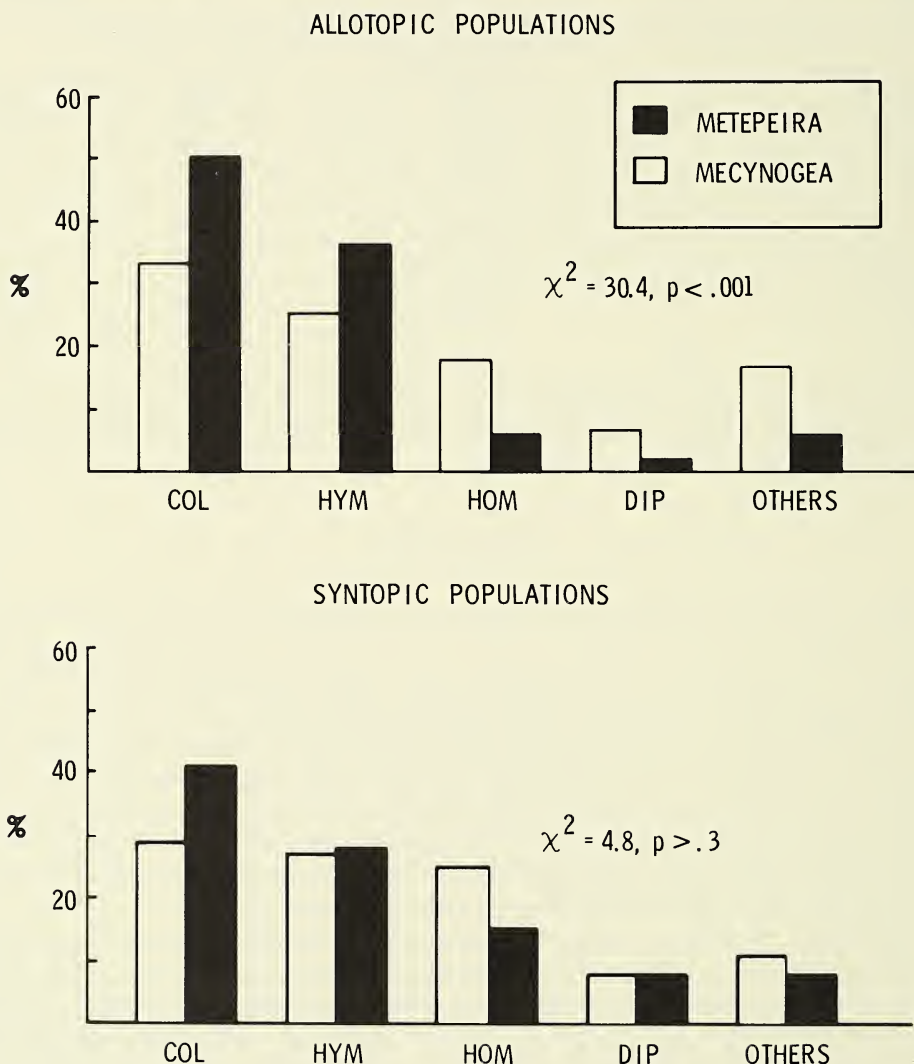


Fig. 1.—Relative representation of the major orders of prey in the webs of *Mecynogea* and *Metepeira* in allotopic and syntopic populations. Larvae, and prey which could not be identified to order, are not included. For *Mecynogea* 149 and 90 prey were identified from allotopic and syntopic populations, respectively; corresponding totals for *Metepeira* were 162 and 106. COL = Coleoptera, HYM = Hymenoptera, HOM = Homoptera, DIP = Diptera, and OTHERS = Odonata, Lepidoptera, Hemiptera, Orthoptera and Neuroptera. The χ^2 statistic is a test of independence of species and prey order in a 2×5 contingency table. The statistic tests whether *Mecynogea* and *Metepeira* differed significantly in the relative proportions of the major insect orders found in their webs. Numbers of prey in the latter orders were combined because analyzing any of them separately produced an expected value < 5 in at least one of the two contingency tables of species $\times$ prey order.

the much finer mesh of the former's web suggests that it might have more small insects in its diet. Such does not appear to be the case. Our schedule of examining webs may have allowed the basilica spider to consume very small prey entirely without being detected. However, predictions from optimal foraging theory and studies of the feeding behavior of other orb-weavers (Schoener 1971, Riechert and Luczak 1982) suggest that such small, energetically poor prey would not comprise the major portion of a mature basilica spider's diet.

We undoubtedly failed to detect some small prey of both species. Furthermore, the spiders may not have extracted the same fraction of the available energy from the different types of prey that did comprise our samples. Also, we collected prey primarily during daylight hours. Thus the insects observed being fed upon and the discarded exoskeletons collected from the webs reflect the diet of each species but are not identical to it. This lack of complete correspondence presents no problem of interpretation, though, because the goal of the research was to compare the filtering properties of webs with markedly different structures. The aim was to uncover the effect of web structure upon diet, not to measure the actual diet of each species.

The similarity of the diets of the basilica and labyrinth spiders cannot lead to a general conclusion that web characteristics play no role in setting a spider's diet. In a recent review article, Riechert and Luczak (1982) summarize many of the studies that demonstrate the extent to which different species of web builders, though polyphagous, tend to

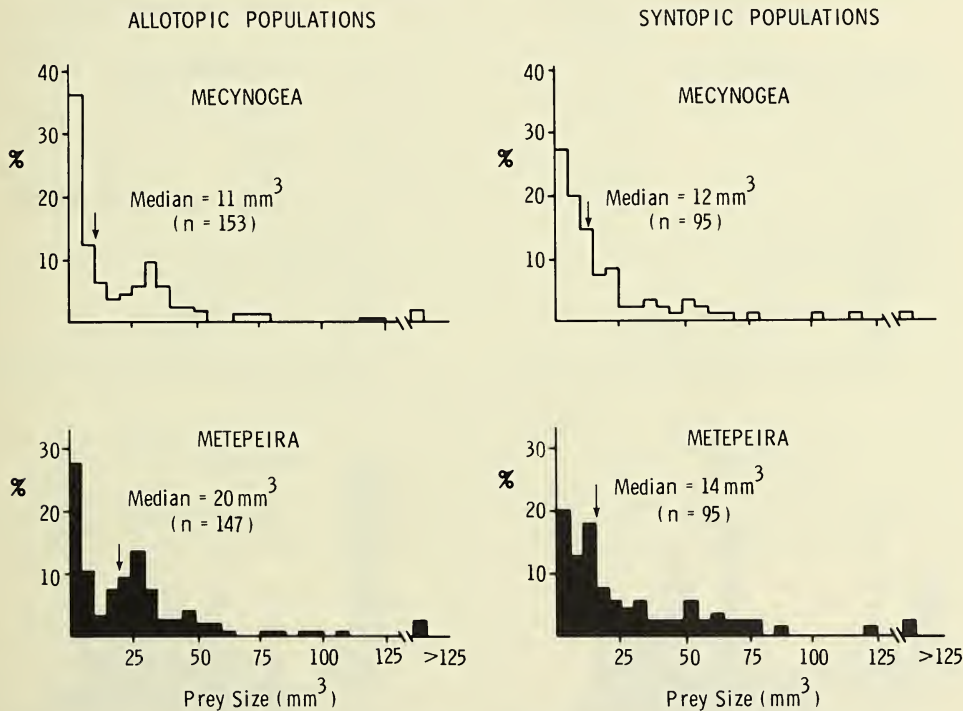


Fig. 2.—Sizes of prey captured by *Mecynogea* and *Metepeira* in the allotopic and syntopic populations. Prey size differed significantly between the allotopic populations (p of $\chi^2 < 0.05$, median test); however, differences between syntopic *Mecynogea* and *Metepeira* populations were not statistically significant (p of $\chi^2 > 0.1$, median test). [Note that the number of prey identified to order (Fig. 1) does not equal the number whose size was determined, because some prey could be identified to order but not measured accurately, or vice versa.]

capture different prey. They point out, though, the difficulty in evaluating the web's role in determining the observed dietary differences, since most of the studies were conducted by different investigators at different times or places and thus cannot be compared directly. Several recent studies do permit one to generalize about the extent to which the diets of syntopic web-builders differ. Uetz *et al.* (1978) found that the size and taxa of prey differed significantly between two similar old-field spiders, *Argiope aurantia* and *A. trifasciata*. The investigators related these differences at least partly to the larger body size and mesh size of *A. aurantia*. On the other hand, Taub (1977) found that the diets of these species overlapped broadly and did not differ significantly in taxa of prey. Taub did find that *A. aurantia* tended to feed on larger prey, and she presents some data which suggest that the filtering properties of the webs may contribute partly to differences in mean prey size. Brown (1981) studied these *Argiope* spp. in different areas and found that the extent to which the diets differed was variable. He found no pattern to suggest that their diets are substantially and consistently different. Other studies also conclude that the diets of closely related syntopic orb-weavers overlap extensively. Kajak (1965) found that syntopic *A. cornutus* and *A. quadratus* select basically the same taxa and size of prey. *Araneus quadratus* and *Argiope bruennichi* also capture prey taxa in the same proportions when the spiders co-occur (Nyffeler and Benz 1978). The pattern emerging from these studies is that diets of closely related syntopic species are very similar, and that even when they differ statistically, the diets still broadly overlap.

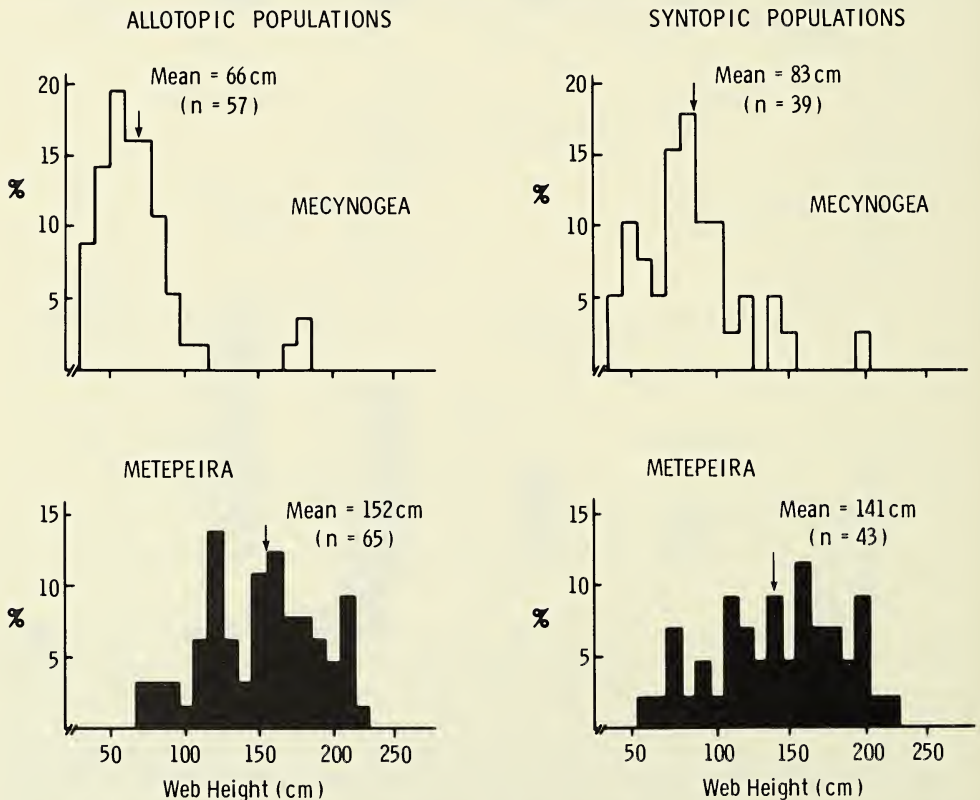


Fig. 3.—Height of the web from the ground of *Mecynogea* and *Metepeira* in the allotopic and syntopic populations. In both populations *Metepeira* built its web significantly higher than *Mecynogea* (p of $\chi^2 < 0.001$ for median test for both allotopic and syntopic comparisons).

The previous research discussed above has compared the prey of species with webs more similar in structure than those spun by *Mecynogea* and *Metepeira*. Riechert recently compared the prey capture of three quite different syntopic web-builders: a scattered-line weaver, a sheetline weaver, and an orb-weaver which inhabit sandstone rock faces. A chi-square test of the taxonomic composition of the prey that encountered these webs and were attacked by the spiders revealed statistically significant differences among the three species. However, substantial overlap in several major prey taxa did occur, and examining the prey taxa that account for the dietary differences suggests that “...location on the cliff face rather than web type itself is responsible for the filtering” (Riechert and Luczak 1982). They suggest that different types of webs capture different prey taxa because the webs require different habitat features for their construction. Any partitioning of prey taxa would thus result primarily from webs being placed in different micro-habitats rather than from different filtering properties. In our study spiders in the syntopic populations captured similar prey even though the species differed significantly in micro-habitat utilization. The large overlap in the diets of the basilica and labyrinth spiders in syntopy contrasts with Riechert’s finding of statistically significant differences in the diets of syntopic species. The greater similarity in diets uncovered in our study may reflect a greater homogeneity of physical features, and hence prey distribution, at slightly

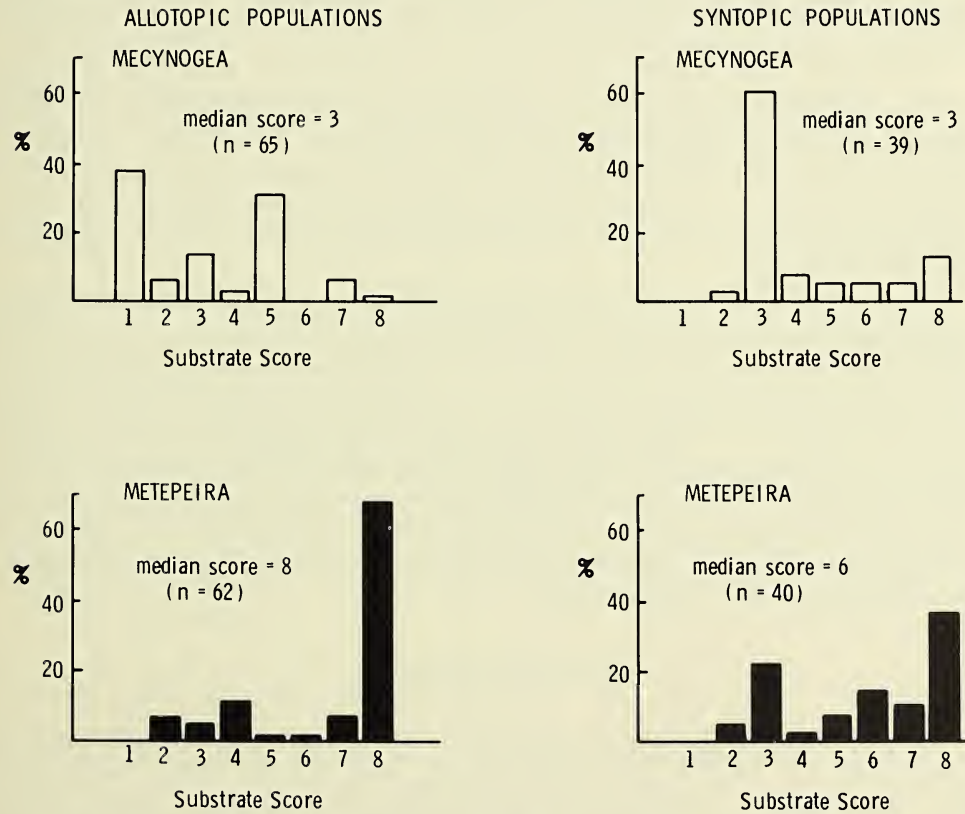


Fig. 4.—Utilization of different substrates for web construction by *Mecynogea* and *Metepeira* in the allotopic and syntopic populations. Rigidity of the substrate increases with increasing score. (Refer to text for details of the scoring procedure.) *Metepeira* built its web on more rigid substrate than did *Mecynogea* in both allotopic and syntopic populations (p of $\chi^2 < 0.001$ for median test for both comparisons).

different heights and areas of a forest compared with differences in prey distribution associated with the more marked physical discontinuities of rock faces.

Other research also suggests that differences in microhabitat utilization and factors other than web properties are the major causes of dietary differences. Olive (1980) discovered that the diets of *Argiope trifasciata* and *Araneus quadratus* converged when the spiders built their webs in more similar microhabitats as the season progressed. In a two-year study, Horton and Wise (1983) found that the diets of *Argiope trifasciata* and *A. aurantia*, though statistically different, were more similar in 1980 than the previous year in the same field and time of season. Mean web heights and spider sizes were also closer in 1980, which may explain much of the convergence in diet.

Our results are consistent with the conclusion that differences between microhabitats influence prey capture more than differences in web structure. Syntopic populations of *Mecynogea* and *Metepeira* were more similar than the allotopic populations in web height and the type of vegetation used for web support. Convergence of these niche parameters in the two species was statistically significant. Prey size and taxonomic composition of the diet were also more similar when the species were syntopic, though the apparent convergence was not statistically significant for either aspect of the diet. These differences in the statistical significance of the convergence in syntopy reflect the fact that parameters of the feeding niche were more similar for allotopic populations than were aspects of the spatial niche; hence for the sample size of this study, almost identical diets in syntopy would have been required for the convergence to be significant statistically.

Divergence in one or more niche parameters in syntopy is often cited as indirect evidence of interspecific competition. Our study provides no such evidence of competition. On the contrary, the results indicate that the species not only fail to shift their niches in response to the presence of the other, but that major parameters of the niche converge in syntopy. A manipulative field experiment conducted the same year in a nearby area uncovered no evidence of interspecific competition between *Mecynogea* and *Metepeira* (Wise 1981).

Studies of prey partitioning conducted to date lead to several generalizations. Statistical differences do sometimes exist between syntopic web builders in size and type of prey captured. These differences reflect differences in spider size and web mesh. Differences also result from different attack behaviors once the prey has hit the web (Olive 1980). However, separation is partial when statistically significant. Broad overlap in diet is the general pattern, even when web architecture is quite different. The location of the web, its size, and the behavior of the spider on the web appear to affect a spider's diet more than the filtering properties of its web. It thus becomes difficult to argue that avoidance of exploitative competition for food is the primary reason syntopic species have evolved structurally different webs.

ACKNOWLEDGMENTS

We wish to acknowledge the contribution to this research of the Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, which provided undisturbed research sites. The University of Maryland Computer Science Center provided support for data analysis. The research was supported by National Science Foundation Grant DEB 77-00484.

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AERIAL DISPERSAL BY MYGALOMORPH SPIDERLINGS (ARANEAE, MYGALOMORPHAE)

Frederick A. Coyle

Department of Biology
Western Carolina University
Cullowhee, North Carolina 28723

ABSTRACT

Ballooning, a form of dispersal rarely seen in mygalomorph spiders, was observed one early spring day in about 30 *Sphodros* spiderlings. After ascending a stump, each spiderling became airborne by dropping and hanging from a dragline which then gradually lifted and lengthened in the breeze, broke at its attachment point, and served as the ballooning thread. Although less effective than the aerial dispersal mechanisms of many araneomorph spiders, this technique can nevertheless produce higher and longer flights than Bristowe and others have suspected.

INTRODUCTION

Although ballooning is a common dispersal mechanism for many kinds of araneomorph spiders, it is presumably only rarely employed by non-araneomorph spiders. I am aware of only five published accounts of ballooning or pre-ballooning behavior in non-araneomorph spiders. Enock (1885) and Bristowe (1939) each observed spiderlings of *Atypus affinis* Eichwald (Atypidae) leaving their maternal tubes on warm, early spring days, trailing draglines, and ascending plants, an apparent prelude to ballooning. Enock (1885) described how some of the spiderlings ascended single-file to the top of a 3 m tall garden stake and "were blown off into mid-air, still keeping a hold upon their endless silken cords, until they became attached to other sticks" which they ascended, only to be blown off onto the ground. Muma and Muma (1945) witnessed similar pre-ballooning behavior by spiderlings of another atypid, *Sphodros rufipes* (Latreille), under laboratory conditions. Although the Mumas reported that the spiderlings climbed upward from the maternal web in single-file, forming a heavy band of silk with their draglines, and then ballooned, they did not describe the ballooning process. Baerg (1928) described how groups of *Ummidia carabivora* (Atkinson) spiderlings (Ctenizidae) disperse during March by walking single-file from the maternal burrow over the ground and up into a tree, leaving behind a conspicuous silk trail. He reported that, once in the tree, each spiderling proceeded "to spin out a thread of silk," but he did not actually observe ballooning. Main's (1957) observations that captured spiderlings of *Conothele malayana* (Doleschall) "produced copious amounts of goassamer," led her to postulate dispersal by ballooning for this widespread ctenizid species which is closely related to *Ummidia*. Although strongly suggesting that these four mygalomorph species do balloon, these observations are incomplete and have understandably been treated with great caution (Bristowe 1939,

Gertsch and Platnick 1980). Consequently, the following account of my fortunate encounter on March 22, 1982, with ballooning *Sphodros* spiderlings (probably *Sphodros atlanticus* Gertsch and Platnick) is important.

RESULTS

The 30 spiderlings that I observed were the last of a larger number of spiderlings that had emerged earlier that day from their maternal tube attached to the west side of a 1 m tall hawthorn stump in a 30 m wide strip of pasture between a hardwood forest and my house, 5 miles south of Cullowhee, North Carolina. I observed the spiderlings from 4:30 pm until the last spiderling departed 47 minutes later. The weather was clear and warm (70°F) with a breeze coming from the west. All these spiderlings were maneuvering on or very near a silk platform composed of draglines which they and their siblings had deposited during their pre-ballooning activity. This silk sheet (Figs. 1 and 2), which was 30 cm long and 11 to 15 cm wide, covered and spanned the spaces between the ends of the three branches (two main and one secondary) which formed the top of the stump. The sheet was thickest around the edges. A band of silk 1 to 1.5 mm wide extended from the upper end of the maternal tube up along the trunk surface to the platform and probably marks the ascent route followed by most or all of the brood.

Ballooning was accomplished in the following manner: Each spiderling would walk along the sheet ascending each slope it encountered, finally arriving, in most cases, on the tip of the smallest branch (Figs. 1-4), which was the most upwind and nearly the highest point on the stump. If not yet on the edge of the sheet, the spiderling would walk to the edge. It would then tilt its cephalothorax upward, lift its first two or three pairs of legs off the silk, and extend them out from the edge. Then the spiderling would drop 5 to 15 cm down from the edge on its dragline. Frequently, during or after such a drop, the breeze would force the spiderling against the trunk, in which case it would ascend the trunk to the platform and repeat the orientation and dropping process. These unsuccessful launches produced the abundance of roughly vertical threads running from the platform edge to the trunk surface (Fig. 3). Elongate holes in the sheet near its highest point (Fig. 4) were probably cut by some spiderlings and used as short-cuts to the upper surface of the platform after unsuccessful ballooning attempts. Sometimes a spiderling would return to its launch site at the platform edge simply by climbing up its dragline, a slower and clumsier process than the dragline climbing I have observed in some araneids. Occasionally, after dropping, a spiderling would not drift into the side of the trunk, but would be blown past and away from the trunk surface. Such a spiderling would then, from time to time, lengthen its dragline, and the force of the breeze would incline the line more toward the horizontal each time. Eventually the dragline would become long enough that the force of the breeze would break it near its point of attachment to the platform and the dragline and the attached spiderling would drift through the air.

Trajectories varied among the eleven spiderlings which I watched as they became airborne. Three drifted downward at the start of their flight and probably landed in the grass 5 to 10 m downwind from the stump. Four rose slowly as they ballooned, but I lost sight of them 5 to 10 m downwind from the stump. One rose steeply at a 30° to 40° angle but I lost sight of it about 4 m downwind from the stump at an altitude of about 3 m. I tracked one ballooning spiderling 20 m before it was lost from view at a height of 4 m. Two ballooning spiderlings drifted into the top of a 1.2 m tall dead weed 0.5 m

downwind from the stump. These then used this plant, which was covered with draglines from earlier balloonists, as a launch site for additional flights.

DISCUSSION

This method of ballooning is clearly different from the common araneomorph method described by Bristowe (1939) and many other authors: "The spider stands on tip-toes, pivoting its body round to face the wind, [tilts its abdomen upwards,] squeezes out a little silk, which is rapidly hauled out by the wind without any assistance from its hind legs, and then, when the pull on the threads from the upward air-current is sufficient, away floats the spider" (Bristowe 1939). A second, less common, but similar mode of araneomorph ballooning is described by McCook (1890). Bristowe (1939) claims that the ballooning threads of araneomorphs are produced by a different pair of spinnerets than is the dragline, and he, like Jonathan Edwards more than 200 years earlier (Smyth 1890), described how an araneomorph may spin these ballooning threads while hanging from its dragline. The spider and its ballooning threads are eventually bouyed up into the air with enough force that the dragline breaks and the spider becomes airborne. I am reasonably confident that the *Sphodros* spiderlings I observed were not taking flight in this manner, for although I could usually see the dragline before and sometimes after launching, I did not see other threads extending from the spiderling.

The *Sphodros* method of ballooning, which involves dropping and hanging from a dragline that is lifted and lengthened by the breeze, breaks near the substrate, and serves

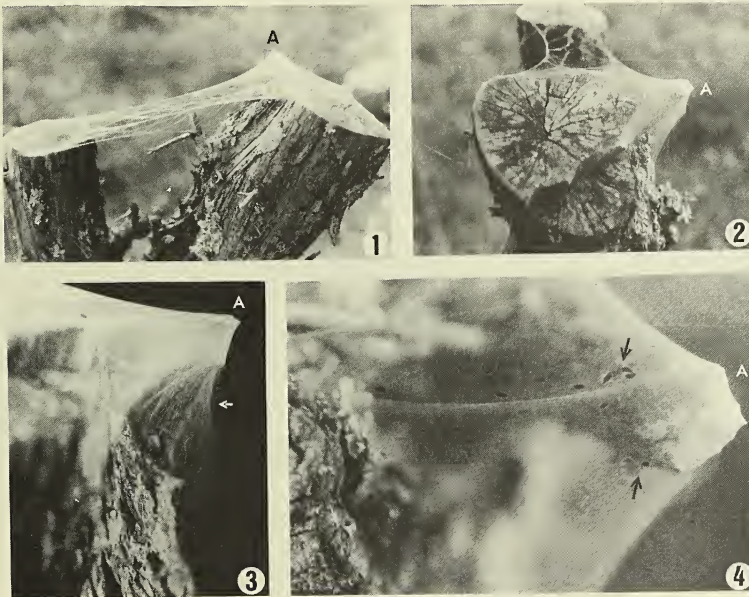


Fig. 1-4.—Ballooning platform constructed by *Sphodros atlanticus* spiderlings: 1, looking slightly down on platform into the wind; 2, looking slightly down on platform, wind coming from the right; 3, dragline threads (arrow) extending downward from primary launch site to side of trunk. These threads were left by spiderlings that were blown into the trunk after dropping from the platform edge. 4, close-up view of upper surface of platform near small branch tip showing holes (arrows) cut by some spiderlings returning to the upper surface. A, tip of small branch from which most of the spiderlings attempted to launch themselves during the course of my observations.

as the ballooning thread, has also been observed in dysderid and segestriid spiderlings by Bristowe (1939, 1958). This is probably a more primitive and shorter distance form of ballooning than that practiced by higher araneomorphs; although it is clear, at least for *S. atlanticus*, that this method can produce longer and higher flights than Bristowe (1939, 1958) had suspected. If, as I have observed, these spiderlings repeat the ballooning process after drifting into tall vegetation, moderately long distance dispersal is possible even in the forest habitats that many *Sphodros* species frequent. This aerial dispersal mechanism produces the interesting intrademe distribution patterns of *S. rufipes* (Coyle and Shear 1981) and *S. atlanticus*, whose tubes are widely scattered, with seldom more than one tube per tree. Similar burrow distribution patterns that I and others (W. J. Gertsch, pers. comm.) have observed in *Ummidia* species are not surprising in light of the evidence that *Ummidia* spiderlings balloon. In contrast, the highly clumped burrow distribution patterns common for antrodiaetid (Coyle 1971) and many other mygalomorph spider taxa, suggest that these spiders do not balloon.

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NOTE ADDED IN PROOF. On 12 March 1983 I observed another ballooning platform on the same stump. Its good condition and the fact that it was almost totally destroyed within three more days suggest that it was formed a day or two earlier during a period of warm sunny weather. The fact that its position and form were virtually identical to the previous year's platform indicates that this new brood of spiderlings performed the same ballooning behavior patterns I have described for the previous year's brood.

A REVIEW OF THE GENUS *TANGAROA* (ARANEAE, ULOBORIDAE)

Brent D. Opell

Department of Biology, Virginia Polytechnic Institute and
State University, Blacksburg, Virginia 24061

ABSTRACT

Characteristics of the genus *Tangaroa* are reviewed and the new species, *T. beattyi*, is described and compared with *T. dissimilis* (Berland) and *T. tahitiensis* (Berland). Cladistic analysis shows the first two species to be most closely related. The tetraspermathecate female genitalia of this genus show no evidence of fertilization ducts and appear to represent a transition state between haplogyne and entelegyne grades of organization.

INTRODUCTION

When Berland (1924) described the first *Tangaroa* species he remarked that it was aberrant and named it accordingly, *Uloborus dissimilis*. The unique characters he recognized were reduced anterior lateral eyes, the absence of abdominal tubercles characteristically found in uloborids, and the simple form of the male palpus. In mistaking mature females for subadults, he acknowledged a fourth character of the genus, the externally unmodified female genital region. The significance of these features was not formally recognized until Lehtinen (1967) established the genus *Tangaroa*. The genus was later restricted by removal of *U. waitakerensis* Chamberlain and further characterized as having haplogyne female genitalia and a presumptive male stridulatory apparatus consisting of an endite file and two setal picks on the cymbium (Opell 1979).

The purpose of this paper is to review the taxonomy of the genus and to present further evidence that female genitalia lack fertilization ducts and are, therefore, in the traditional sense, haplogyne. The former treatment is necessitated by discovery of a new *Tangaroa* species, and the latter is made possible by the availability of well preserved specimens of this species.

METHODS AND MATERIALS

Specimens of *Tangaroa beattyi* were fixed for about one month in Bouin's fixative, rinsed in several changes of 0.1 M sodium cacodylate buffer (pH 7.3), dehydrated through a graded series of acetone, and imbedded in Spurr's epoxy resin. Prior to examination, 1 μ m thick sections made with a Sorvall JB-4 microtome were stained with one percent toluidine blue in one percent borate buffer.

Scanning electron microscopy was performed on Bouin's-fixed specimens which were dehydrated in acetone, critical-point-dried, and vacuum evaporator coated first with carbon and then with gold-palladium.

Tangaroa Lehtinen

Tangaroa Lehtinen 1967:266, 391; Opell, 1979:474. Type species by original designation *Uloborus tahitiensis* Berland, 1934:323. The genus name is feminine.

Diagnosis.—Both males and females are distinguished from all other uloborids by having reduced anterior lateral eyes which are represented only by small pigment spots (Figs. 11, 18). Males are further characterized by the presence of a distal crook on the ventral surface of tibia I (Figs. 10, 14), a palpal femur whose length is at least three times that of the palpal trochanter (Fig. 2), and a folded or lobed distal cymbial region (Figs. 2, 9). Unlike males of other uloborid genera, those of *Tangaroa* lack an embolus guide and have a flattened embolus (Figs. 2, 9). Like *Waitkera* and *Polenecia* males, they have a presumptive stridulatory apparatus consisting of a file on the endite's lateral surface and distal cymbial picks (Figs. 1, 2). In *Tangaroa* there are two and in *Waitkera* three (Opell 1979, fig. 28) macrosetal picks. *Polenecia* males have two macrosetal picks plus an apical cymbial spine (Opell 1979, fig. 47).

Tangaroa contains the only uloborid females that lack external modifications of the genitalic area. Such modifications are slight, but discernable in *Waitkera* (Opell 1979, fig. 30). Openings are located on the posterior surface of the genital region, within the confines of the epigastric furrow. Each opening leads to two spermatheca, the ventral one bearing a slight swelling or lobe that appears to be a site of secretory activity (Figs. 6, 19, 21).

Tangaroa tahitiensis (Berland)

Figures 8-10, 18, 19; Table 1

Uloborus tahitiensis Berland 1934:323, 331, figs. 1, 6. Male holotype and three female paratypes in Muséum National d'Histoire Naturelle, Paris, examined.

Diagnosis.—This is the largest known *Tangaroa* species (Table 1). Males are distinguished by the first leg having seven macrosetae in or adjacent to the ventral tibial notch, four prolateral femoral macrosetae, and seven dorsal tibial macrosetae (Fig. 10). Females are characterized by having three prolateral macrosetae on femur I and by lacking dark pigment in the spiracular region.

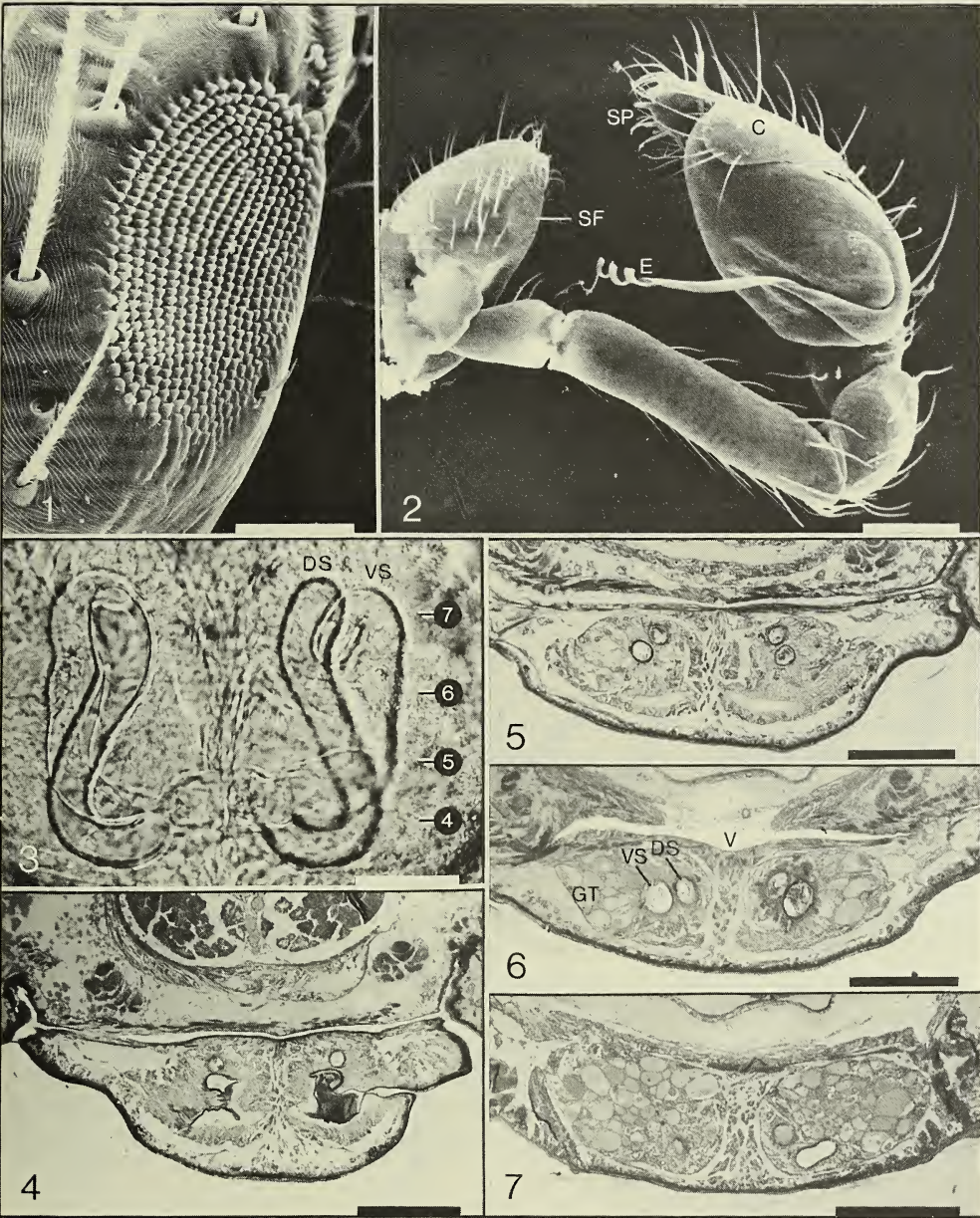
Distribution.—Tahiti, Society Islands; Rapa, Tubuai Islands.

Tangaroa dissimilis (Berland)

Figures 11-14, 20-22; Table 1

Uloborus dissimilis Berland 1924:176, figs. 18-20. Male paratype from Kone, female paratype from Mont Canala, New Caledonia.

Note.—Type specimens appear to have been lost. Illustrations and diagnosis are based on a male (AR 115) from Mt. Alempe (513 m.), Epi, New Hebrides, collected 21 Nov.

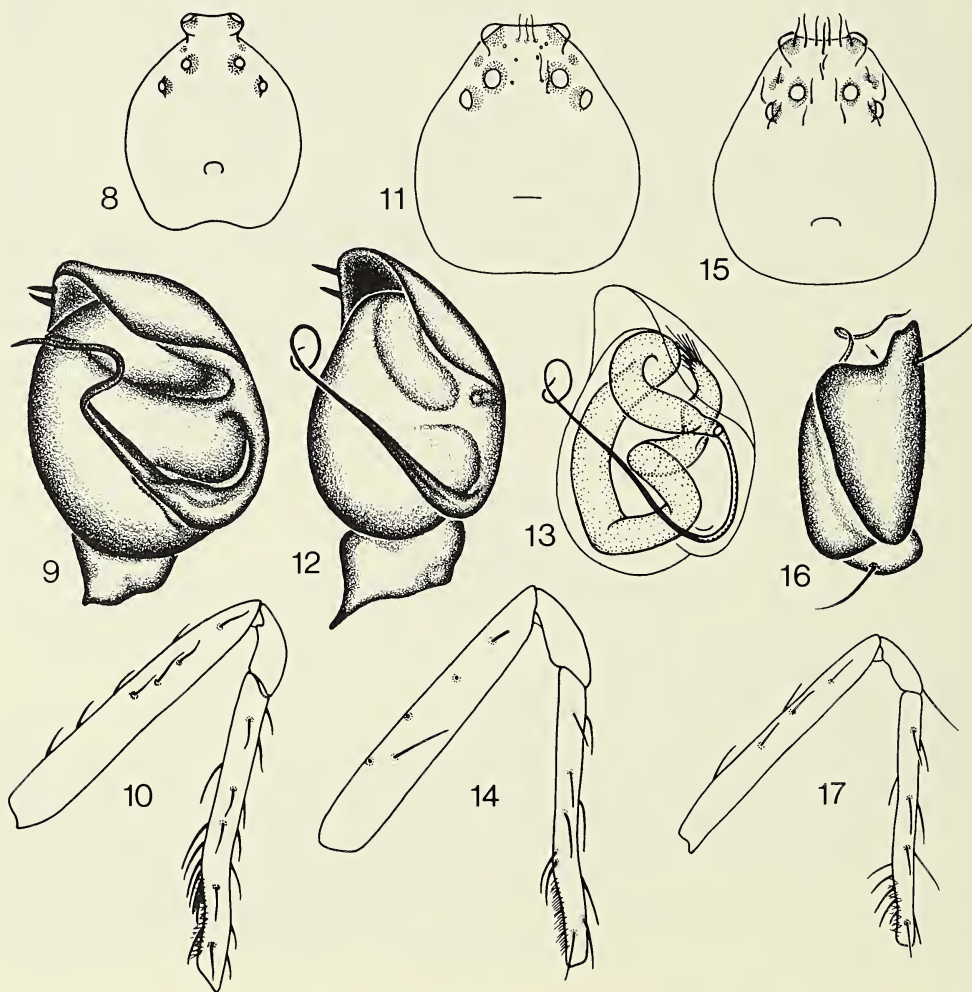


Figs. 1-7.—*Tangaroa beattyi*, new species: 1, Retrolateral view of male left endite showing stridulatory file; 2, Retrolateral view of male left palpus showing cymbium (C), embolus (E), and stridulatory picks (SP) and file (SF); 3, Dorsal view of cleared female genital region showing dorsal and ventral spermathecae (DS and VS, respectively); 4-7, Cross sections through female genital region (see Fig. 3 for position) showing spermathecae, glandular tissue (GT), and vagina (V). Scale line in Fig. 1, 20 μ m. Fig. 2, 100 μ m, and Figs. 3-7 50 μ m.

1945 and deposited in the Muséum National d'Histoire Naturelle, and a female from Espiritu Santo, New Hebrides, collected May 1944 and deposited in the American Museum of Natural History.

Diagnosis.—This species is intermediate in size between *T. tahitiensis* and *T. beattyi* (Table 1). Males are distinguished by the first leg having two macrosetae adjacent to the distal tibial notch, two dorsal femoral macrosetae, and five dorsal tibial macrosetae (Fig. 14) and by having 11 ocular macrosetae (Fig. 11). Females are characterized by having three retrolateral macrosetae on the first femur, by having a pigmented spiracular area (Fig. 22), and by lacking genital macrosetae.

Distribution.—New Caledonia and New Hebrides.



Figs. 8-10.—*Tangaroa tahitiensis* (Berland): 8, Male carapace; 9, Retrolateral view of male left palpus; 10, Prolateral view of male left first femur, patella, and tibia.

Figs. 11-14.—*Tangaroa dissimilis* (Berland): 11, Male carapace; 12, Retrolateral view of male left palpus; 13, Retrolateral view of cleared male left palpus showing sperm ducts; 14, Prolateral view of male left first femur, patella, and tibia.

Figs. 15-17.—*Tangaroa beattyi*, new species: 15, Male carapace; 16, Median view of male palpus showing notched cymbium (arrow); 17, Prolateral view of male first femur, patella, and tibia.

Tangaroa beattyi, new species

Figures 1-7, 15-17, 23-24; Table 1

Types.—Male holotype and female paratype from nipa palms in swamp near Fanif, Yap Island, Caroline Islands, collected 14 April 1980 by Joseph Beatty. Male and female paratype from mouth of cave, Yap Island, collected 28 April 1980 by James Berry. Holotype and paratype in the Bishop Museum, others in the Museum of Comparative Zoology. This species is named for Joseph Beatty who along with James Berry collected it.

Diagnosis.—This is the smallest described *Tangaroa* species (Table 1). Males are distinguished by having three or four macrosetae in and adjacent to the ventral notch of tibia I (Fig. 17), by having 19 ocular macrosetae (Fig. 15), and by having a cymbial notch (Figs. 2, 16). Females are characterized by having an inverted, comma shaped pigment area around the PME's (Fig. 23), by having a pigmented spiracular region, and by having 15-17 genital macrosetae (Fig. 24).

Description.—Male. Total length 1.98 mm, carapace length 0.84 mm. When alive, members of both sexes were blue to light purple in color. Color patterns described here are those of alcohol preserved specimens. Carapace tan with gray posterolateral margins and gray circles around eyes (Fig. 15). Ocular region beset with about 19 stout setae (Fig. 15). Sternum tan with faint gray patches near coxae. Legs tan, the venter of each femur with a small, distal gray region. First leg macrosetae as presented in Table 1 and Fig. 17. Abdomen light tan with four faint, paraxial gray spots, a gray posterior tip, a ventrolateral gray stripe, and gray spiracular and epigastric regions. Male palpus (Figs. 2, 16) with a conspicuous retrolateral cymbial notch. The coiled embolus tip that appears in the palpi of both alcohol preserved and critical-point-dried specimens is probably an artifact of initial preservation. The embolus tip is least convoluted in *T. tahitiensis* (Fig. 9), indicating that distortion may increase as the embolus becomes thinner.

Female. Total length 2.06 mm, carapace length 0.76 mm. Carapace tan with posterolateral margins and gray circles around eyes, the PME's with an anterior gray extension (Fig. 23). Sternum tan with a posterior gray tip. Legs tan, each tibia with a faint gray distal ring. First leg setae as described in Table 1. Dorsum of abdomen light tan with posteriorly open V at its anterior margin, one or two pairs of central, paraxial gray spots, and a gray posterior tip. Lateral surface with a ventral gray stripe. Venter with light gray spiracular region and broad gray book lung patches (Fig. 24). Genital region slightly concave and beset with stout setae (Fig. 24). A pair of spermathecae extend from each of two posterior dorsal genital openings (Fig. 3). The dorsal spermathecae are more slender and expand only slightly, whereas the ventral pair expand near the center (at which point secretory tissue appears to surround them) and terminate in a narrowed loop (Figs. 3-7).

Natural History.—In both the field (J. Beatty and J. Berry, personal communication) and laboratory, *Tangaroa beattyi* immatures and mature females constructed small, horizontal orb-webs.

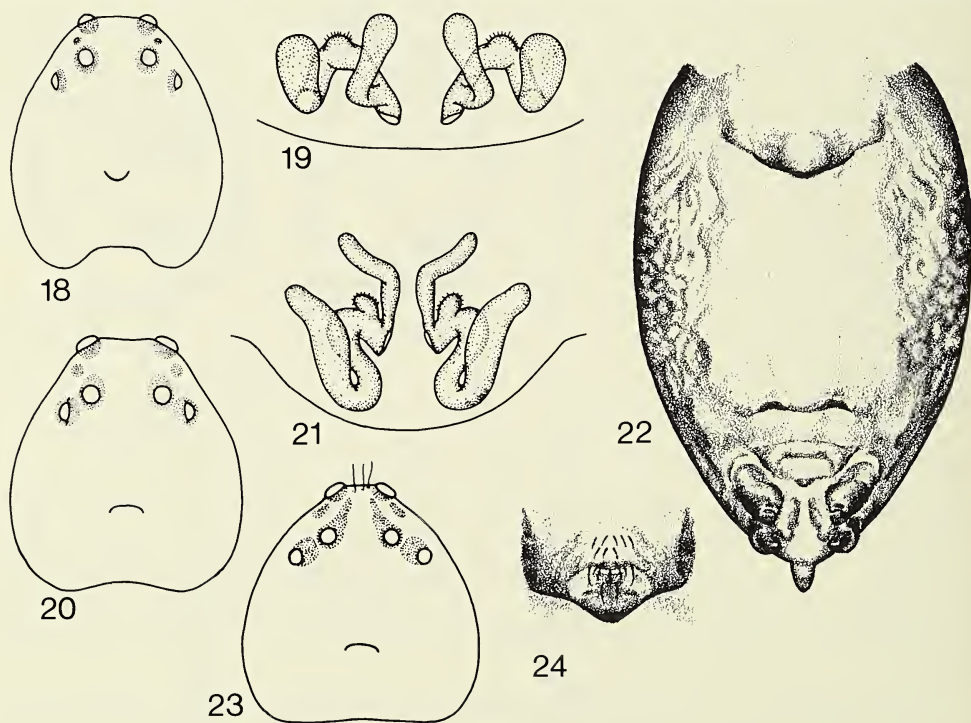
Distribution.—Known only from the type locality in the Caroline Islands.

DISCUSSION

Despite their geographical separation, a cladistic analysis shows *T. beattyi* and *T. dissimilis* to be more closely related to one another than either is to *T. tahitiensis* (Fig.

25). Because immatures have fewer setae than adults the lowest number of prolateral, dorsal, and retrolateral femoral and tibial macrosetae is considered to be the plesiomorphic state of these characters. The absence of ocular and genital macrosetae is, likewise, considered plesiomorphic. Of less certain polarity is the presence of a cymbial notch in males and spiracular area pigment in females. In both cases the absence of these features is considered plesiomorphic; although, a reversal of this polarity would change neither the cladogram nor the number of evolutionary steps required to explain it. A minimum of 18 evolutionary steps is required to explain distribution of the 12 2-state and three 3-state characters used in this analysis. The cladogram presented in Figure 25 requires a total of 18 character state changes.

The presumptive stridulatory apparatus of *Tangaroa* is found only in the family Uloboridae and here only in the three most primitive genera (Opell 1979). Its absence in other uloborids may indicate an increased reliance on web- rather than air-borne vibrations during courtship. Stridulatory devices have originated a number of times in spiders (Legendre 1963, Rovner 1975) and this particular device is probably an apomorphic character of early uloborids. The only alternate hypothesis is that the file represents the modified lateral region of a multiple row serrula similar to that found in *Hypochilus* (Platnick 1977, figs. 14, 15). The latter hypothesis is unlikely, as *Tangaroa*



Figs. 18-19.—*Tangaroa tahitiensis* (Berland): 18, Female carapace; 19, Dorsal view of cleared female genital region.

Figs. 20-22.—*Tangaroa dissimilis* (Berland): 20, Female carapace; 21, Dorsal view of cleared female genital region; 22, Ventral view of female abdomen.

Figs. 23-24.—*Tangaroa beattyi*, new species: 23, Female carapace; 24, Dorsal view of cleared female genital region.

females have only a single row serrula and males have a similar serrula along the endite's anterior margin. Additionally, it is ruled out by Platnick's (1977) conclusion that all non-hypochiloid Araneomorphae are derived from ancestors with simple serrulae. This conclusion was confirmed by examining eight (numbers 1, 2, 3, 4, 6, 9, 10, 12) of the twelve characters used by Platnick (1977, fig. 7) to evaluate the relationship of hypochiloids and other Araneomorphae. Of these, *Tangaroa* shares only the presence of tetraspermathecate female genitalia with the *Hypochilus* - *Ectatosticta* lineage.

The tetraspermathecate female genitalia of *Tangaroa*, like those of some other higher araneomorphs such as *Tetragnatha* (Levi 1981, Wiehle 1963) present a problem. Although their genitalia lack fertilization ducts and are similar to the primitive araneomorph pattern (Platnick and Gertsch 1976) found in *Hypochilus* (Kraus 1978, Gertsch 1958, 1964), Platnick (1977) has shown that all araneomorphs except *Hypochilus*, *Ectatosticta*, and *Hickmania* are derived from ancestors with a single pair of spermathecae. This suggests a fundamental difference between primary and secondary tetraspermathecate genitalia.

In bispermathecate spiders each spermatheca must store, nourish, and, when eggs are laid, probably activate quiescent spermatozoa (Kanwar 1967, Osaki 1969, Reger 1970, Sharma 1950, Sharma and Gupta 1956). In tetraspermathecate spiders derived from these ancestors, doubling of the spermathecae could be an adaptation either to increase volume for sperm storage or to partition storage and activation functions. Addition of proximally connected spermathecae in spiders which had already come to rely on a single pair seems a less efficient means of increasing storage volume than expanding the existing spermathecae. It would also introduce the problem of dividing the flow of semen from the male's embolus, which, judging from its length in *Tangaroa*, is probably inserted past the junction of the two spermathecae. As Kraus (1978) has noted, tetraspermathecate (2+2) neocribellates lack a wide, interconnecting vulval atrium that would permit the lateral flow of semen. In spiders which lack fertilization ducts this evidence favors origin of a second pair of proximally connected spermathecae to serve in sperm activation or another supplementary secretory function such as producing material which plugs the external genitalia of some spiders.

Small glands associated with the ventral spermathecae of *Tangaroa* (Figs. 19, 21) are similar to those borne on the lateral or terminal surfaces of *Hypochilus* and mygalomorph spermathecae (Brignoli 1980, Forster and Wilton 1968, Kraus 1978), indicating that the ventral pair is probably the primary pair.

Cross sections of *T. beattyi* female genitalia (Figs. 4-7) indicate that in the specimen examined only the right side was inseminated. On this side material is present in the lower (posterior) part of the ventral spermatheca (Fig. 4) and apparent secretory activity, as indicated by more darkly stained cytoplasm, surrounds the central region (Fig. 6) of both lateral spermathecae. Walls of the ventral spermathecae stain more darkly than those of the dorsal spermathecae.

Tangaroa appears to provide an example of a group intermediate between the haplogyne and truly entelegyne condition, a grade of organization similar to that referred to by Brignoli (1978) and Wiehle (1967) as the semientelegyne condition. The male's embolus can be inserted directly into a spermathecal duct, but, lacking fertilization ducts, female genitalia open into the confines of the epigastric furrow where exiting sperm are provided certain and protected contact with ova. Levi (1981) suggested that simple *Tetragnatha* female genitalia may be explained by cheliceral interlocking during courtship and the opportunity this affords for palpal alignment. Although courtship has not been reported

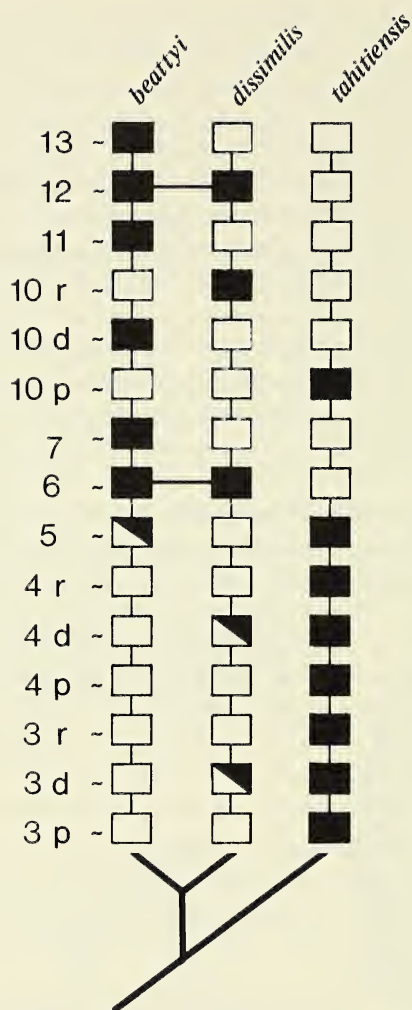


Fig. 25.—Cladogram of *Tangaroa* relationships. Numbers correspond to characters presented in Table 1, p, d, and r indicating prolateral, dorsal, and retrolateral macrosetae, respectively. White rectangles denote plesiomorphic character states and darkened and partially darkened rectangles apomorphic character states.

for *Tangaroa*, the first tibial crook unique to males of this genus may allow the male to firmly grasp the female and provide an analogous explanation for alignment of simple male and female genitalia.

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I thank Drs. Joseph Beatty and James Berry for providing specimens and Drs. Norman Platnick and Michel Hubert for lending material from the American Museum of Natural History and the Muséum National d'Histoire Naturelle, respectively. Drs. Willis Gertsch and Herbert Levi provided helpful comments on an earlier draft of this paper. This study was supported in part by National Science Foundation Grant DEB-8011713.

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NOMENCLATURAL NOTE

Opinion 1245.—The International Commission on Zoological Nomenclature ruled under their plenary powers that (1) the type material of *Linyphia tenebricola* Wider, 1834, be set aside and that the neotype proposed by Locket, Millidge and van Helsdingen, 1978, be accepted; and (2) that the specific name *tenebricola* Wider, 1834, as published in the binomen *Linyphia tenebricola*, and as interpreted by reference to the neotype accepted under the plenary power in (1) above, be placed in the Official List of Specific Names in Zoology with the Name Number 2849 (Bull. Zool. Nomencl., 40:39, 1983).

On 5 April 1983 the Commission gave six month notice of the possible use of its plenary power in the following case: Z. N. (S.) 2223—Request for a ruling to correct homonymy in names of the family-groups based on *Myrmecia* Fabricius, 1804 (Insecta, Hymenoptera, Formicidae) and *Myrmecium* Latreille, 1824 (Arachnida, Araneae, Clubionidae). The Commission welcomes comments and advice from interested zoologists (Bull. Zool. Nomencl., 40:43, 1983).

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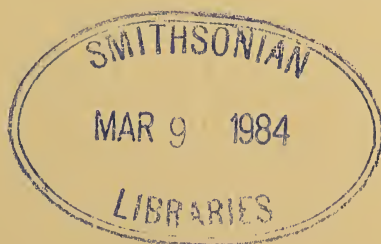
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**MICROHABITAT SELECTION AND LOCOMOTOR ACTIVITY
OF *SCHIZOCOSA OCREATA* (WALCKENAER)
(ARANEAE: LYCOSIDAE)**

Alan B. Cady¹

Department of Zoology
Ohio University
Athens, Ohio 45701

ABSTRACT

Direct observations of the wolf spider *Schizocosa ocreata* (Walckenaer) in a deciduous woods during its breeding season indicated that soil moisture, deciduous leaf litter, and herbaceous vegetation influenced the patterns of their distribution and movement. Areas of high soil moisture, non-compressed litter, and a micro-canopy of herbaceous vegetation comprised the microhabitat with highest spider density. Spiders tended to travel greater distances in the drier patches, suggesting that the increased level of locomotion was related to increased searching for favorable environments. *S. ocreata* was found to aggregate at a litter patch size of 625 cm².

This lycosid appeared to employ a sit-and-wait foraging strategy based on the relationships of spider movement and microhabitat selection. A sex ratio of 1:1 differed from those previously obtained by pitfall trapping methods. Movement and distance information from direct observations of spiders provided support to the previous hypothesis of greater motility of male lycosids.

INTRODUCTION

Microhabitats and their associated microclimates play an important role in determining the local distribution patterns of small terrestrial animals (Odum 1971, Krebs 1972). Mainly due to their large surface area to volume ratio, arthropods are greatly influenced by even minor changes in temperature and humidity.

Leaf litter structure and associated herbaceous vegetation control the spatial distributions of litter dwelling spiders (Vlijm and Kessler-Geschiere 1967, Edgar 1971, Uetz 1975, Kronk and Riechert 1979), mainly through the amelioration of environmental extremes (Hagstrum 1970, Den Hollander and Lof 1972, Edgar and Loenen 1974, Riechert and Tracy 1975). Furthermore, the structure of leaf litter attracts potential prey, provides areas of reduced temperature fluctuations, retains moisture, and creates refugia for hunting spiders (Uetz 1975). Herbaceous vegetation of the woodland floor forms a "micro-canopy" over the litter layer, further modifying the microenvironment. Temperature and humidity were shown to be critical factors influencing microhabitat selection for a number of spider species (Nørgaard 1951, Williams 1962, Cherrett 1964, Duffey 1966,

¹Present address: Department of Biology, Lindenwood College, St. Charles, Mo. 63301.

Sevacherian and Lowrie 1972, Richert and Tracy 1975), and field studies provide evidence that lycosoid spiders select favorable thermal environments (Hallander 1970a, Riechert and Tracy 1975). Microhabitat selection has been shown to provide spatial separation and reduce cannibalism for closely related lycosid spiders (Hallander 1970b, Hagstrum 1970, Edgar 1971).

The ability of lycosids to move great distances (Richter et al. 1971) enables them to encounter many different microhabitats in their lifetime. It was formerly thought that wolf spider locomotor activity was related to their foraging behavior. However, Enders (1975) suggested that these predators may adopt a sit-and-wait strategy (Schoener 1971) to secure their food. This hypothesis predicts that movements of lycosids should be lowest within areas of favorable environmental conditions. Also, Ford (1977) found that the sit-and-wait strategy adopted by *Pardosa amentata* was more energetically efficient than actively hunting. Therefore, locomotor activity would reflect the spiders' search for suitable microhabitats or resting sites, and not necessarily their hunting tactics. Furthermore, predators may increase locomotor activity in areas where little prey is encountered, resulting in more movement within poorer habitats than in higher quality ones.

The present study describes influences of microhabitat structure on the local patterns of distribution and locomotor activity for the wolf spider *Schizocosa ocreata* (Walckenaer). My observations indicate that *S. ocreata* actively selects its microhabitat, and that its distribution and locomotor activity are related to available moisture and other physical features as leaf litter, spring seepage, the presence of saplings, and herbaceous vegetation.

STUDY SITE AND METHODS

Schizocosa ocreata primarily occupies deciduous leaf litter substrates in moist areas across the eastern United States (Kaston 1948), although it is also found in drier uplands (Uetz and Denterlein 1979). The data were collected from a deme located at Stroud's Run State Park, Athens County, Ohio, USA from 13 March thru 16 June, 1977.

Study Site.—The study site was within a second growth temperate deciduous forest (Odum 1971) composed mainly of broadleaf hardwoods, and was located in a small ravine formed by an intermittent stream. A spring seepage drained through the site down a 5-25% southwest slope towards the stream. At times the water flow was copious, inundating a 1 m wide (0.5-1.0 cm deep) swath down the slope. The soil was a heavy montmorillonite-type clay, with a shallow (0.0-2.0 cm) mull humus layer. Leaf litter covered the entire area. Its depth varied from 0.0-6.0 cm, and consisted of the previous autumn's leaves [mainly oaks (*Quercus* spp.), beech (*Fagus grandifolia*), and sycamore (*Platanus occidentalis*)]. The litter structure varied from Heatwole's (1961) Class I curled to Class II thick. Litter was deepest in depressions, around the bases of saplings or shrubs, and where herbaceous stems prevented it from being scattered by the wind. Litter was compressed and moist in the area of the spring seepage. Most of the herbaceous vegetation was associated with the drier litter; very little grew in the seepage. The following herbaceous plants occurred in the ground layer: Muhly (*Muhlenbergia* sp.), Peruvian Daisy (*Galinsoga* sp.), Virginia Creeper (*Parthenocissus quinquefolia*), Plantain (*Plantago* sp.), and Wood Sorrel (*Oxalis* sp.).

Two 2x2 m plots each enclosing distinctly different physical features were placed within the study site to assess spider locations and activities within different microhabitats. Plot I contained two areas of deep litter and herbaceous vegetation separated by the

spring seepage. Nine saplings (5-15 cm dia.) were present. Two crayfish (*Orconectes*) burrows on the plot's boundaries were indicative of the soil's wetness.

No surface water occurred at any time in Plot II; seepage affected a small part of one border only during rainy periods. Two saplings (7-8 cm dia.) were present while herbs covered most of the plot.

Methods.—The investigation was based upon direct field observations of free ranging wolf spiders, as this method yields more detailed data on the exact locations, activities, and duration of behaviors than pitfall trapping. The frequency, duration, direction, and location of locomotory activity were used as a bio-assay for microhabitat preference.

Galvanized wire outlined the plots' boundaries, and tags painted with light-reflective paint (to facilitate night observations) were placed at 10-cm intervals along the wire. The habitat structure (litter, saplings, spring seepage, rocks, wood, and herbaceous vegetation) of each plot was mapped on the basis of a 10-cm grid using the point intercept method. "Full litter" was recorded if litter at a point was not compressed and over 1 cm deep; bare ground, compressed litter, or litter under 1 cm deep was scored as "sparse litter." Soil moisture was determined gravimetrically after drying.

Observation sessions were four hours long during each day of the study. The entire diel period was sampled to ascertain any diurnal-nocturnal differences in spider activity. This resulted in approximately 100 hrs of observations on adults and 140 hrs on immature spiders. The plots were divided into 4 sections, and each section was closely scrutinized for 15 min. Thus, one plot was completely surveyed each hour. A headlamp was used at night. When a spider was sighted, its position and movements during a two minute observation period were mapped, and the spider's sex and time of sighting were noted. A relative measure of the distance a spider moved during the two minute observation period was obtained by measuring the mapped route of a spider to the nearest 0.5 cm. Spiders were placed into 3 groups (male, female, total [males + females]), and further division was made based upon their relative degree of activity (stationary, moving, total [stationary + moving]).

Block size analysis of variance was employed to investigate the distribution patterns of spiders and litter types within each plot. Greig-Smith (1952, 1961, 1964) and Kershaw (1960, 1964) described and developed this method which involves partitioning the total variance of a grid or line of quadrats. A peak in mean square (variance) above the mean indicates maximum heterogeneity is found among the quadrats at that block size. Therefore, peaks in mean square at a particular block size indicate aggregation or clumping of spiders at that block size.

A rectangle and square system (Greig-Smith 1952) was used for analysis of pattern, where block sizes 1, 4, and 16 were square, and block sizes 2, 8, and 32 were rectangular. The basic quadrat (block size 1) was 156.25 cm². Associations between spider and litter distributions in each plot were measured by block size analysis of covariance (Kershaw 1961).

Other statistical procedures were from Sokal and Rohlf (1969) and Conover (1971).

RESULTS AND DISCUSSION

The results will be presented and discussed in three sections. The first deals with associations between the microhabitat and distribution of *Schizocosa ocreata* (microhabitat selection), the second pertains to locomotor activity of the spiders in relation to

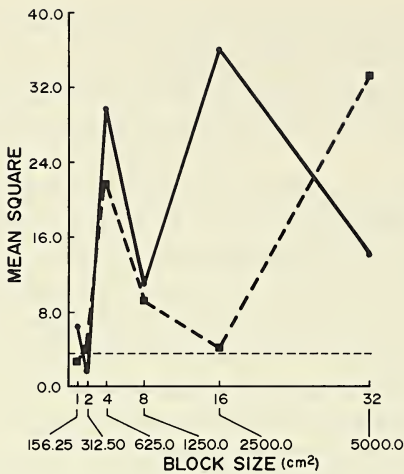


Fig. 1—Variance plotted against block size for Grouped + Stationary *Schizocosa ocreata* (dashed line) and full litter (solid line) in Plot I. Horizontal dashed line indicates mean. A peak in mean square above the mean indicates clumping at that block size. Peaks occur at block sizes 4 and 32 for spiders and block sizes 4 and 16 for full litter.

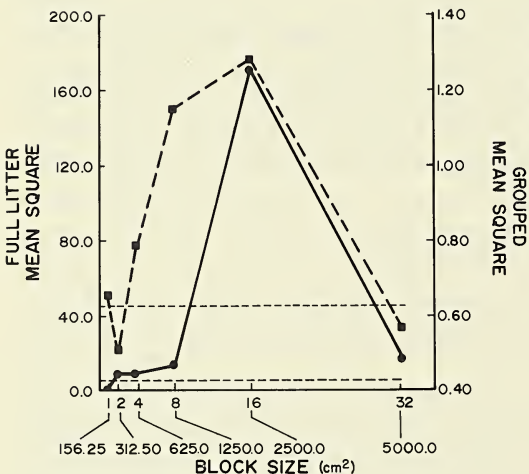


Fig. 2.—Variance plotted against block size for Grouped *Schizocosa ocreata* (dashed line) and full litter (solid line) in Plot II. Horizontal dashed lines indicate means. A peak in mean square above the mean indicates clumping at that block size. Peaks occur at block size 16 for spiders and full litter.

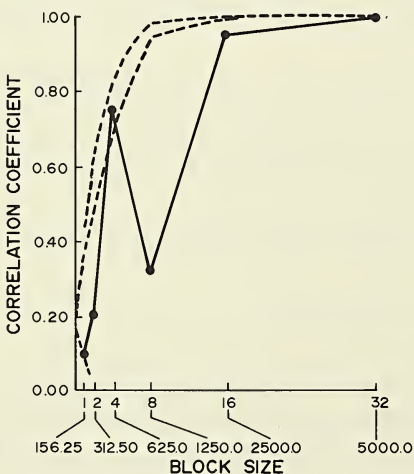


Fig. 3.—Results of correlation coefficients computed on covariances between stationary *Schizocosa ocreata* and full litter in Plot I. Dotted lines represent upper and lower confidence limits ($P < 0.05$ and $P < 0.01$). A peak outside a confidence limit indicates correlation at that block size (block size 4 in this case). The converse of this figure is identical in the negative (for sparse litter and stationary spiders).

Table 1.—Densities, means (number/16 quadrats in each plot), variance, and Coefficients of Dispersion (CD = variance/mean) for litter types and *Schizocosa ocreata* within Plots I and II. A significant CD indicates a clumped distribution (as tested with the Poisson distribution). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

CATEGORY	NUMBER	MEAN $\pm$ SE	VARIANCE	CD
<i>PLOT I</i>				
FULL LITTER	165.75	10.36 $\pm$ 1.7	45.06	4.35***
SPARSE LITTER	214.25	13.39 $\pm$ 1.7	44.86	3.35***
STAT. SPIDERS	109	6.81 $\pm$ 1.7	47.81	7.02***
MOVING SPIDERS	44	2.75 $\pm$.51	4.09	1.52
MALE SPIDERS	86	5.36 $\pm$ 1.1	19.99	3.73***
FEMALE SPIDERS	67	4.19 $\pm$ 1.1	20.53	4.90***
TOTAL	153	9.56 $\pm$ 2.1	68.16	7.13***
<i>PLOT II</i>				
FULL LITTER	218.75	13.67 $\pm$ 2.0	63.98	4.68***
SPARSE LITTER	174.25	10.89 $\pm$ 2.0	65.67	6.03***
STAT. SPIDERS	25	1.56 $\pm$ 2.0	2.39	1.53
MOVING SPIDERS	15	.94 $\pm$.30	1.69	1.79
MALE SPIDERS	21	1.31 $\pm$.30	1.50	1.14
FEMALE SPIDERS	19	1.19 $\pm$.30	1.29	1.09
TOTAL	40	2.50 $\pm$.50	3.60	1.44

microhabitat, and the third considers differences between male and female spiders relative to their activity and microhabitat selection.

Microhabitat and Spider Distribution.—The overall density (over the entire study) of *S. ocreata* was higher in Plot I than Plot II (Table 1, $\chi^2 = 66.16$, $P < 0.001$, $df = 1$). More spiders were found in full litter than in sparse litter (Table 2). Spiders in Plot I aggregated at block sizes 4 and 32 (Fig. 1), whereas those in Plot II aggregated only at block size 16 (Fig. 2). However, only the spiders in Plot I were significantly clumped (Table 1, Coefficient of Dispersion). The overall distribution of full litter and spiders were positively correlated in both plots (Table 3), and the spatial patterns of spiders were positively correlated with full litter and negatively correlated with sparse litter in Plot I at block size 4 (Fig. 3). The significant clumping of spiders and their correlation with full litter in Plot I not found in Plot II, suggests the presence of some factor(s) which influenced aggregation within Plot I which was not found in Plot II. The soil and litter layer in Plot I was moister than that of Plot II (Mann-Whitney U Test, $T = 0.00$, $P < 0.001$, $N = 4$), and full litter was more strongly associated with herbaceous vegetation in Plot I (Fig. 4). Therefore, it appears that areas of high soil moisture, full litter, and herbaceous vegetation provided the preferred microhabitat for *S. ocreata* (i.e. Plot I). Because spiders were correlated with full litter at block size 4, the habitat patch size in this particular area was approximately 625 cm².

Hagstrum (1970) found a direct correlation between the depth of litter and the density of the lycosid spider *Tarentula kochi*, and Uetz (1976) showed that the number of wandering spider species was positively correlated with litter depth and negatively correlated with the percent reduction of litter due to flooding.

In the present study, flooding from the spring seepage similarly reduced the amount and depth of litter, and spider density was lower in the seepage area than in other areas of Plot I ($\chi^2 = 65.88$, $P < 0.001$, $df = 1$). Herbaceous growth shades and anchors litter, and

Table 2.—Chi-square test for goodness-of-fit comparing frequencies of stationary, moving, and total *Schizocosa ocreata* in full vs. sparse litter. One degree of freedom for all tests. All chi-squares adjusted for proportional amounts of full and sparse litter. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	FULL LITTER	SPARSE LITTER	χ^2
<i>STATIONARY</i>			
MALES	53	14	23.99***
FEMALES	44	23	7.12**
BOTH	97	37	20.84***
<i>MOVING</i>			
MALES	19	21	.130
FEMALES	11	8	.545
BOTH	30	29	.099
<i>TOTALS</i>			
MALES	72	35	13.77***
FEMALES	55	31	7.29**
BOTH	127	66	20.84***

saplings allow litter to collect around their bases. Thus, where these two vegetational features occur, a deep, stable litter layer is created, providing a favorable area where *S. ocreata* and their prey may live. It is evident that the physiognomy of the woodland floor exerts an important effect upon the patterns of local distributions of *S. ocreata*.

Locomotor Activity and Microhabitat Selection.—If this spider was actively selecting the most suitable microhabitat, less locomotor activity should be observed within preferred areas. The data suggests that full litter is a preferred habitat. There were more stationary than moving spiders within full litter (data in Table 2, $\chi^2 = 16.05$, $p < 0.001$), and the distance which spiders travelled was positively correlated with sparse litter (Table 3). The percentage of spiders found moving in sparse litter was higher than that found in full litter, and the percentage of stationary spiders was higher in full litter than within sparse litter (Table 4). Stationary spiders were positively correlated with full litter and negatively correlated with sparse litter (Fig. 3). These results show that spiders moved farther and more often in sparse litter than full litter, and suggests that microhabitat selection is cued by the environmental and biological conditions which exist within full litter.

Spiders tended to move across areas of sparse litter and stop upon contact with a patch of full litter (Table 5). If a spider began movement in sparse litter it tended to continue moving, whereas ones initiating movement in full litter did not move very far, terminating the bout of activity within full litter (Table 5). Hallander (1967) suggested that substrate type influences the level of activity of *Pardosa chelata* and *P. pullata*, since there was less locomotion in a preferred substrate (leaves) compared to non-preferred substrates. In the present study, moving spiders were found more often in the less preferred microhabitat, and stationary spiders occupied the areas with more cover. Therefore, stimulation of activity or non-activity by the substratum probably was a major factor underlying *S. ocreata*'s microhabitat selection. Spiders in non-preferred (unfavorable) areas may be stimulated to move, increasing the chance of encountering a preferred (favorable) microhabitat. Once there, stimulation to move would be less, and the spider would be more likely to remain in a favorable spot.

Table 3.—Phi coefficient (nonparametric measure of association, Conover 1971) showing correlation of stationary, moving, and distance moved by *Schizocosa ocreata* with litter types. N = 426. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	MALES	FEMALES	TOTAL
FULL LITTER			
Stationary	0.2267***	0.1526***	0.2865***
SPARSE LITTER			
Moving	0.0284	0.0065	0.0287
Distance moved	0.1103*	0.0080	0.1088*

Males vs. Females.—During the time of this study, it is likely that female spiders were searching for prey while male spiders were searching for females (Vlijm and Richter 1966). This was reflected in the differential microhabitat selection and levels of locomotor activity found between the sexes. Female *S. ocreata* tended to remain within full litter whenever possible, as they were found most often in full litter (Table 2). The distribution of stationary females was positively correlated with that of full litter (Table 3). Laboratory observations have shown that female *S. ocreata* tended to stay under the paper “cage cards” and inside of water vials, whereas males were mostly on top of the cards and not in the vials (Table 6). These results indicate that females in the field may be responding to cover and higher humidity provided by full litter.

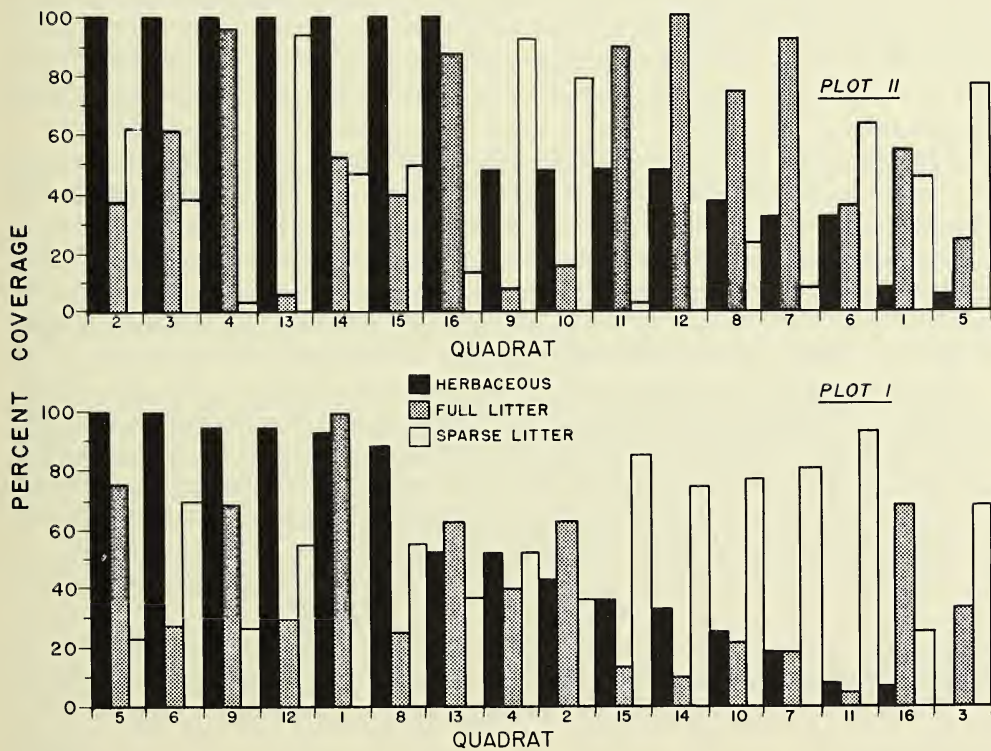


Fig. 4.—Percent coverage comparisons of herbaceous vegetation, full litter, and sparse litter for each quadrat in Plots I and II.

Table 4.—Percentages of stationary and moving male and female *Schizocosa ocreata* within full and sparse litter. T = the test statistic for equality of two percentages; Sokal and Rohlf (1969). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	PERCENT WITHIN FULL LITTER	PERCENT WITHIN SPARSE LITTER	T
<i>STATIONARY</i>			
MALES	42.70	21.20	3.08***
FEMALES	34.6	34.8	0.03
BOTH	76.0	56.1	2.80***
<i>MOVING</i>			
MALES	14.9	31.8	2.67***
FEMALES	8.6	12.1	0.76
BOTH	24.0	43.9	2.80***
<i>SAMPLE SIZES</i>			
MALES	72	35	
FEMALES	55	31	
TOTAL	127	66	

Reproductive success could be enhanced by utilizing a microhabitat which supplied numerous prey. Uetz (1976) found that potential prey species richness was positively correlated with deciduous leaf litter depth. Therefore, females which occupy deeper litter would have a higher probability of encountering prey. Spaces under the litter offered a warm, moist area where time of activity would be extended (Uetz 1979), and which also provided a favorable site for egg incubation. Thus, by selecting the proper microhabitat, female *S. ocreata* are able to exploit the enhanced environmental and energy-supplying characteristics of full litter.

Male spiders moved more than females. The mean relative distance travelled by males was greater than that for females (male mean = 22.03 cm, female mean = 14.36 cm; Mann-Whitney Text $T = 807.5$, $P < 0.01$, $N = 80$), and a higher percentage of males were moving than were females within sparse litter (males = 72.41%, females = 27.59%, test statistic = 2.237, $P < 0.01$). These direct observations of *S. ocreata* support earlier hypotheses (based on studies utilizing pitfall trapping) of elevated male lycosid motility during the breeding season. The higher motility of male lycosids is attributed to the

Table 5.—Frequencies of continuation or termination of a bout of locomotor activity by *Schizocosa ocreata*. A. The direction of movement (i.e. from one litter type to the other) and the frequency of either stopping or continuation of movement upon crossing that boundary. B. Frequencies of locomotory bouts occurring entirely within one litter type during a 2 min. observation period. Stopping indicates the spider halted before the end of the observation period, no stop shows the spider was still moving after 2 min. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	STOP	NO STOP	χ^2
A. Full to Sparse	3	7	1.6
Sparse to Full	12	2	7.14**
B. Within Full	17	4	8.05**
Within Sparse	2	19	13.76***

Table 6.—Frequencies of male and female *Schizocosa ocreata* on top or under paper cage cards (on bottom of cages) or inside water vials. (Data courtesy of Gail Stratton, Univ. of Cincinnati.)

	ON TOP	UNDER
MALES	79	18
FEMALES	46	69
$\chi^2 = 37.35 \quad df = 1 \quad P < 0.005$		

male's search for females during the reproductive period (Vlijm and Richter 1966, Hal-lander 1967, Richter et al. 1971). Typical sex ratios resulting from pitfall trap studies usually show a higher proportion of males than females. The sex ratio obtained from these direct observations was approximately 1:1 (males = 107, females = 86, $\chi^2 = 2.28$ ns, $df = 1$; ratio = 1:1.2). Therefore, results obtained from direct observations give a truer representation of the actual sex ratio than studies using pitfall trapping, which typically indicate more males.

The sit-and-wait foraging strategy (Enders 1975) would predict the optimal location for foraging by *S. ocreata* would be in full litter. The above results support this hypothesis. This wandering spider preferred the favorable environmental conditions found in full litter over those found in sparse litter for their resting (and hunting) spots. Spiders under full litter were protected from environmental extremes and easy predation (birds and spider wasps [Pompilidae]), and were in an area of high prey density. Sparse litter did not provide avenues for quick escape from predators or adverse physical conditions, so spiders would not have been expected to remain on sparse litter for prolonged periods of time. Most moving spiders seen in or on sparse litter continued moving (Table 5).

Proper microhabitat selection by *S. ocreata* is probably important to courtship and subsequent meeting of the sexes. Stridulation is part of the acoustic display performed in the courtship of many lycosid spiders (Rovner 1975). A stridulating male *S. ocreata* may be heard over 2 m away when he is on full litter. The large leaves found there supply a good "sounding board" for amplification and conductance of acoustical signaling. It has been shown for other lycosids that the female spider orients to and approaches hidden stridulating males (*Lycosa rabida*, Rovner 1967; *Schizocosa rovneri*, Stratton and Uetz 1981). *S. ocreata* is closely related to *S. rovneri*, and probably responds in a similar fashion. Therefore, a male spider courting on full litter would have a higher probability of attracting a female than a male on sparse litter. A higher density of females occurs within full litter, and the substratum is well suited for acoustical displays. This, along with possible chemical attraction (Tietjen 1979) and the physical characteristics of full litter may explain the aggregations of *S. ocreata* found in and on full litter.

Schizocosa ocreata utilizes a heterogeneous habitat by actively selecting the microhabitat most favorable for their reproductive and environmental requirements. We now need information on what takes place under the litter, for these animals live in three dimensions. Mating was observed on the surface only twice, so it probably occurred under the litter most of the time. This is only one example of the many different activities which are not easily seen by surface observations, and indicates a direction for future investigations.

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CHEMICAL SIGNALS BOUND TO THE SILK IN SPIDER COMMUNICATION (ARACHNIDA, ARANEAE)

Chantal Roland

Laboratoire de Biologie du Comportement
Université de Nancy I
B. P. 239
54506 - Vandoeuvre-les- Nancy Cedex - France

ABSTRACT

The silk produced by the spider contributes not only to the security of the individual (dragline, retreat, eggsac) and to capture prey (snare) but also plays a role in the exchange of information between individuals. The structured silk constitutes a network favorable to the transmission of vibratory phenomena but a single silk thread can also inform a spider of the presence of a conspecific and of its sexual identity through tactochemical cues. A number of authors have shown, namely in Lycosidae, that the substratum of the female's silk with which a pheromone is associated, triggers off the courtship of the male. Moreover, an individual coming across a dragline can orientate its locomotion according to the identity of the spider which emitted the thread. Results obtained with *Tegenaria domestica* and *T. pagana*, in a T-maze, show that specific female sexual factors associated with the silk enable the male to orient its movements. The nature of these factors has not yet been determined. It is probably a pheromone. In our experimental conditions the specification of these factors appears to be only partial. A male coming across another species' dragline will follow it. But given a choice between a conspecific dragline and a different species' dragline, it will move towards the former. Finally, a male sexual factor able to orientate the female's direction has been demonstrated in *Tegenaria domestica*. The silk-provided tactochemical information allows the spiders to orient themselves towards conspecifics and to adjust their behavior (courtship behavior) according to the conspecifics they may meet. Similar results have been obtained with another species of Agelenidae (*Coelotes terrestris*) and with two species of Araneidae (*Araneus sclopetarius* and *A. cornutus*).

In social spiders there exists the problem of group cohesion which has been studied by using the same techniques.

INTRODUCTION

Communication obviously is necessary in social animals, but it is also needed by solitary animals, at least during courtship and in agonistic interactions (Riechert 1978). The act of communication implies the emission of a signal, its transmission and its reception. Signals transmitting information can be chemical, visual, vibratory or tactile. If it is a chemical signal, it is termed a pheromone. Chemical signals are known to be involved in spider sexual behavior (Krafft and Roland 1980), in parental care (Krafft and Horel 1980) and in cooperative behavior (Krafft 1979). Up until now, experiments in spiders have only demonstrated pheromones that are bound to the silk and to the integument, though the existence of volatile pheromones emitted by female spiders has been suggested by Bristowe and Locket (1926), Millot (1946), Blanke (1973) and Tietjen (1979).

Tacticochemical stimuli are known to be important to the courtship behavior of male spiders representing a variety of spider families (Pisauridae, Bristowe 1958; Salticidae, Crane 1949, Legendre and Llineares 1970, Lycosidae, Kaston 1936, Rovner 1968, Hegdekar and Dondale 1969, Dondale and Hegdekar 1973, Richter and Stolting 1971, Dumais et al. 1973, Farley and Shear 1973, Tietjen and Rovner 1982, Filistatidae, Berland 1912, Araneidae, Blanke 1973, Locket 1926, Dictynidae, Jackson 1978). Various workers have examined the role of silk-bound pheromones in spiders (e.g. Kaston 1936, Dondale 1977). Dijkstra (1976) was the first to use a complex maze to show that males are capable of orienting preferentially to female draglines. Tietjen (1980) used a different technique to show that male lycosids follow females' draglines, something initially investigated by Engelhardt (1964).

Our laboratory has been studying the mechanisms of communication in spiders for a number of years. We have developed a technique for the study of male orientation to silk-bound pheromones: the method takes into account the particular behaviors of various spider families.

METHODS

We adapted a T-maze for use on spiders (Krafft and Roland 1979), which permits the study of sexual attraction in different species of funnel-web builders: *Tegenaria domestica* (Clerck), *T. pagana* (C. L. Koch) and *Coelotes terrestris* (Wider). It was also used to test the response of the araneid, *Araneus sclopetarius* (Clerck). This same technique also allows one to study the chemical factor that causes group cohesion in the social eresid *Stegodyphus sarasinorum* (Karsch).

Our experimental design involves observing the movement of a spider in a T-maze as a function of a stimulus previously placed in the maze. The following stimuli were used:

- 1 — a silk substrate produced by a spider permitted to roam freely in one arm of the maze during a 30-minute period (the other arm of the T was closed off).
- 2 — as in 1, but the silk is removed with a brush.
- 3 — a dragline extracted from an anesthetized (CO₂) spider and placed into the T-maze by the experimenter.
- 4 — airborne odors blown across the arm of the T-maze.

In performing these experiments, we held the environment constant while alternating the experimental arms of the T-maze, right and left. Adults were used in all experiments. Each type of experiment was repeated from 30 to 250 times, chi-square tests were applied to the data to test for significance.

RESULTS

Sexual attraction.—The results of the trials involving a test for sexual attraction are shown in table 1.

Female pheromones: when a female walks in the maze, she appears to modify the environment in a way that influences the orientation of the male (exp. 1). The male is unable to orient (exp. 2) to the female when the silk has been removed. Finally a single thread is sufficient for male orientation (exp. 3). These experiments show that the factor responsible for orientation by the male is bound to the silk.

Table 1.—Sexual attraction. In each experiment a number of individuals (ranging from 30 to 250 were given a choice between stimulus A or B in a T-maze. The significance levels obtained from Chi-Square tests are: ns = not significant, * = 0.05, ** = 0.01, *** = 0.001.

Experiment No.	Sex	Test Situation arm A	arm B	<i>Tegenaria domestica</i>	<i>Tegenaria pagana</i>	<i>Coelotes terrestris</i>	<i>Araneus sclopetarius</i>
1	♂	♀ substrate	none	***	***	***	***
2	♂	♀ substrate (silk removed)	none	ns	ns	ns	
3	♂	♀ thread	none	***	***	***	***
4	♂	♂ substrate	none	ns		ns	
5	♀	♀ substrate	none	ns	ns	ns	
6	♂	♀ substrate	♂ substrate	***		***	***
7	♂	heterosp. ♀ thread	none	**	**		***
8	♂	consp. ♀ thread	heterosp. ♂ thread	***	***	***	**
9	♀	♂ substrate	none	***		*	

It is reasonable to assume that the orientation factor is a pheromone. Preliminary observations made with a scanning electron microscope showed no differences in texture among silk from male and female *Tegenaria domestica*, *T. pagana* and *Coelotes terrestris*.

Males do not show a corresponding orientation to a male substrate (exp. 4) and females do not respond to female substrate (exp. 5). Given a choice between male and female substrates, males further orient only to the female substrate (exp. 6).

These individuals do not respond simply to conspecific silk, as is known for social spiders (see below). Males only show the orientation response to female silk.

To determine whether the latter response is species-specific, a choice was offered between no silk in one arm and female silk of another species of the same family in the other arm (exp 7). The results suggest an absence of specificity in the female sex pheromone. However, given a choice between silk from a conspecific female and from hetero-specific female, the male shows a preference for his own species (exp. 8).

Male pheromone: Until recently, there was a tendency to view sexual behavior in spiders rather rigidly—the male has an active role and the female has a passive role. Lately, a number of observations have indicated that there is an exchange of information between the partners (Platnick 1971, Krafft and Leborgne 1980). Certain facts suggest that males produce a chemical signal for the females and even for other males. According to Ross and Smith (1979), the male's silk in *Latrodectus hesperus* causes a sexual response in the female. Tietjen (1979) supports that males of *Lycosa rabida* may emit an airborne pheromone that modifies the behavior of other males. In our own studies, evidence suggests that the female orients towards a male substrate in *Tegenaria domestica* and *Coelotes terrestris* (exp. 9).

Social attraction.—In social spiders there exists the problem of group cohesion. By using the same techniques as before, we obtained the results seen in table 2.

Social attraction does not depend on an olfactory stimulus in *Agelena consociata* nor in *Stegodyphus sarasinorum* (exp. 1 and 2).

In contrast, the silk of adult female *S. sarasinorum* provides a social cue that stimulates the orientation and the aggregation of conspecific of the same sex (exp. 3). Aggregation is not observed when the silk is removed (exp. 4). The stimulus is bound to the thread. That

Table 2.— Social attraction. In each experiment females of two species of social spiders (*Agelena consociata* and *Stegodyphus sarasinorum*) were given a choice between stimulus A or B in a T-maze. The significance levels obtained from Chi-Square tests are: ns = not significant, * = 0.05, ** = 0.01, *** = 0.001.

Experiment No.	Species	Test Situation		Chi-Square results
		arm A	arm B	
1	<i>Agelena</i>	odor of 5 spiders	none	ns
2	<i>Stegodyphus</i>	odor of 5 spiders	none	ns
3	<i>Stegodyphus</i>	<i>Stegodyphus</i> track	none	***
4	<i>Stegodyphus</i>	<i>Stegodyphus</i> track, silk removed	none	ns
5	<i>Stegodyphus</i>	<i>Stegodyphus</i> thread	none	***
6	<i>Stegodyphus</i>	<i>Araneus</i> thread	none	*
7	<i>Stegodyphus</i>	<i>Stegodyphus</i> thread	<i>Araneus</i> thread	**
8	<i>Stegodyphus</i>	<i>Stegodyphus</i> thread	<i>Amaurobius</i> thread	ns
9	<i>Stegodyphus</i>	<i>Stegodyphus</i> thread	<i>Eresus</i> thread	ns
10	<i>Stegodyphus</i>	<i>Stegodyphus</i> thread	<i>Amaurobius</i> and <i>Eresus</i> threads	*

is, the thread alone is sufficient for the response, as shown in exp. 5, in which we placed a thread from a female into the maze. However, the response may not be species-specific entirely, since, when faced with a choice between silk from *Araneus* and no silk, females selected the *Araneus* silk arm (exp. 6). Female *Stegodyphus sarasinorum* did prefer conspecific silk when offered a choice between that and the silk of *Araneus* (exp. 7). When the choice is between conspecific silk and that of other cribellate spiders (*Amaurobius* and *Eresus*), female *Stegodyphus* had greater difficulty in making the distinction (exp. 8-9 and 10). It appears that draglines of all of these species contain each a part of information that intervene in the orientation of *Stegodyphus*.

DISCUSSION

The results obtained with different species of agelenids and araneids show that males are able to orient to female threads. This orientation depends on a chemical factor that is bound to the silk and which is likely a female sex pheromone.

Several questions still exist. First, in addition to mere detection of the chemical, there may be directional information based on the physical nature of the thread, as was suggested by Tietjen (1977). Next, there is the possibility of the breakdown of the pheromone after a more or less lengthy delay. This could transmit temporal information to the male. If the pheromone is short-lived, the detection of an active thread of a female by the male would indicate that a female is in the immediate vicinity. In lycosids, the pheromone is known to be broken down by moisture such as dew. This was shown by Hegdekar and Dondale (1969), Dondale and Hegdekar (1973), and Gwinner-Hanke (1970). For spiders dwelling in protected habitats, such as *Tegenaria domestica* and *T. pagana* some other mechanism would have to operate. Finally, there is an increased possibility of female location by the males of these web species, if the female leaves the web, thereby providing threads that extend some distance away from the web. Except for the observations by Riechert on *Agelenopsis* (1981) little information exists on the degree of activity exhibited off the web by web spiders.

In *Tegenaria*, we showed that enough specificity exists in the chemical properties of the silk to provide an interspecific barrier. Although under laboratory conditions, the male may follow the thread of a heterospecific female when no other thread is available, he selects a conspecific thread when offered a choice between threads. Perhaps there is common chemical information on the silk among related species. However, isolation and analysis of the pheromone is necessary to determine this. In the sympatric species *Tegenaria domestica* and *T. pagana*, the relative specificity of the pheromone plays an important role in reducing the risk of interspecific encounters. However, in case of an error, vibratory communication between male and female spiders serves as a second mechanism to reinforce the interspecific barrier. (Krafft and Leborgne 1980).

Location of the female is not the only function provided of the pheromone. Males of certain species begin courtship behavior in response to the female's silk, as shown long ago by Bristowe (1926) and others. One can imagine that the effects of chemical stimulation in the male that has contacted female silk could modify the responsive state of the male to yield a selective sensory condition that prepares him to react positively to new stimuli emanating from the female.

As to the social spiders, the information contained in the silk has a very different function in contributing to group cohesion, particularly in keeping the individuals of the society in the nest (Jackson 1978). It is clear from these findings and ideas that silk is important in spider communication, in that it provides the basis for chemical information as well as acting as the carrier of vibratory communication.

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COMPARATIVE ECOLOGY OF TWO LINYPHIID SPIDERS (ARANEAE, LINYPHIIDAE)

Anthony C. Janetos¹

Biology Department
University of Utah
Salt Lake City, UT 84112

ABSTRACT

Frontinella pyramitela, the Bowl and Doily Spider, and *Neriene radiata*, the Filmy Dome Spider, were the two most common linyphiid species in a study of sheetweb weaving and orbweaving guilds in central New Jersey. They differ in size when adult and in the relationship between prey size and spider size, but not in the absolute size of prey taken nor in their tendency to move from websites. Competition for websites is a negligible factor in the system, although the populations may be food-limited. These results are compared with studies by Wise (1975) and Riechert (1976, 1978, 1981).

INTRODUCTION

In the course of a study on the foraging behavior of orbweavers (Araneidae) and sheetweb weavers (Linyphiidae) in central New Jersey (Janetos 1982), I marked numerous individuals of *Neriene radiata* (Walckenaer) and observed several characteristics of their foraging ecology. I also marked and observed another common linyphiid, *Frontinella pyramitela* (Walckenaer), the Bowl and Doily Spider. Here I report observations on both species and compare them to the experimental results of Wise's (1975) study on food limitation.

Both spiders were very common in the habitat in which I worked, and were the primary representatives of the family Linyphiidae. The space-filling webs of *F. pyramitela* and *N. radiata* occupy similar areas in the vegetation. The web of *F. pyramitela* consists of a sheet of silk pulled down into a bowl, with a flat sheet below that and a loose tangle of threads above. The spider runs upside-down on the bottom of the bowl. Small insects hit the loose tangle of threads and fall to the bowl, where the spider captures them from below. The web of *N. radiata* is a sheet of silk that has been pulled up into a dome, lacks a second sheet underneath, but has a loose silk tangle above. The spider runs upside-down under the dome and prey capture is similar to *F. pyramitela*. Thus, these species are ecologically and behaviorally similar in their foraging, i.e., they constitute a guild (Root 1967). I also report data gathered on the guild as an entity, to enable a comparison between the guild and its component species as well as to discover the source of variation in the guild's characteristics.

¹Present address: IPH, Harvard School of Public Health 665 Huntington Ave., Rm. 1308, Boston MA 02115

METHODS

The spiders were marked and censused in the course of a larger field study (Janetos 1982). The study site was the Stony Ford field station in Princeton, NJ, in old fields that were being re-invaded by various shrub and tree species. There was considerable floristic and structural diversity in the study area, but no closed canopy. I marked spiders in their webs by applying a small dot of model airplane paint. Websites were marked by tying a numbered strip of flagging tape onto the vegetation supporting the web. Spiders occasionally ran into the tangled threads or nearby vegetation during marking, but their subsequent behavior did not differ from unmarked individuals. All measurements of spider length, web size and prey size were made with a small plastic millimeter ruler, so that there was a minimum of disturbance by me. Daily censuses were made of all websites marked during the study, whether currently occupied or not. Flying prey were sampled by sticky traps similar in design to those introduced by Eberhard (1977).

Most of the data exhibit non-normal distributions. Statistical tests were thus non-parametric (Siegel 1956).

RESULTS

Figure 1 shows the distributions of body lengths for each species. *Neriene radiata* is the larger of the two (*N. radiata* $\bar{x}$ = 4.8 mm vs. *F. pyramitela* $\bar{x}$ = 3.3 mm, $p < 0.0001$, Mann-Whitney U test). Interestingly, the coefficients of variation of the two distributions are similar (C. V. = 0.23 for *F. pyramitela* and C. V. = 0.15 for *N. radiata*). The variation in size within the guild is mainly due to the difference in average size between *F. pyramitela* and *N. radiata*. The low extreme of the size range is composed entirely of Bowl and Doily Spiders, while the high extreme is composed only of Filmy Dome Spiders. Only in the central part of the size range of the guild is there overlap between the two species.

The sheetweb weavers take more small size classes of flying prey than sampled by sticky traps (Fig. 2; $\chi^2 = 11.5$, $p < 0.05$). Uetz and Biere (1980) argue that such traps are biased in the direction of over-representing large prey. Thus, the linyphiids may take prey as a nearly random sample of their true availability.

The correlation between average prey size and spider size (Fig. 3) is slightly different for the two species. *N. radiata* exhibits very little influence of size on the average size of its prey ($r_s = 0.049$), whereas the body length of *F. pyramitela* is strongly ($r_s = 0.33$) and significantly ($p < 0.01$) correlated with the average size of its prey. The guild as a whole shows strong positive correlations of spider size with average prey size in both field seasons (Fig. 4ab) (1978: $r_s = 0.227$, $p = 0.018$; 1979: $r_s = 0.393$, $p < 0.0001$).

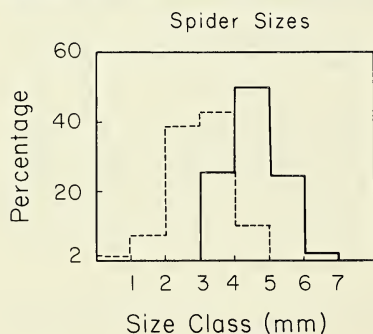


Fig. 1.—Histogram of body lengths of each species. Dashed line: *Frontinella pyramitela*, $\bar{x}$ = 3.3 mm, N = 162. Solid line: *Neriene radiata*, $\bar{x}$ = 4.8 mm, N = 59.

The distributions of residence time at a website for each species appear in Fig. 5. They are similar, although there is a statistically non-significant difference in the mean residence times (5.4 days for *F. pyramitela* and 3.9 days for *N. radiata*). Figure 5 also compares the distributions of residence times of *F. pyramitela* and *N. radiata* with those expected from a hypothesis of random spider movements (Janetos 1982). The Filmy Dome Spider has almost the same distribution of residence times that one would expect if the spider left web sites randomly. The Bowl and Doily Spider does not quite show the expected distribution of residence times. Most of the difference comes at the shortest residence time (1 day) where more cases were observed than expected. However, the rest of the deviations from expectation offer no clue to any pattern of behavior in the spiders. This is in striking contrast to the orbweavers in the same habitat (Janetos 1982).

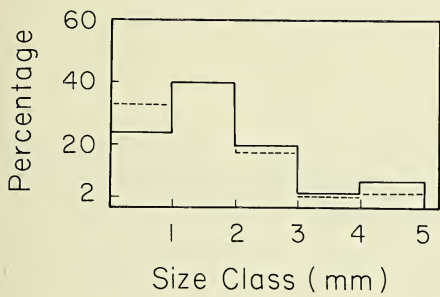
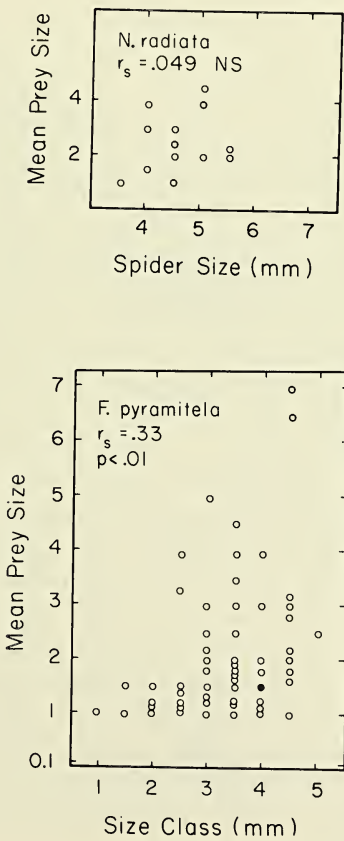


Fig. 2.—Distributions of body lengths of prey. Solid line: prey sampled by sticky traps, $N = 332$. Dashed line: prey observed in linyphiid webs in 1978 and 1979, $N = 462$. Distributions are significantly different, $X^2_4 = 11.5$, $p < 0.05$.

Fig. 3.—Average body length of prey in webs of each species of spider vs. body length of the spider. Upper graph: *Neriere radiata*. Lower graph: *Frontinella pyramitela*. Black dots indicate points where five or more observations overlap.



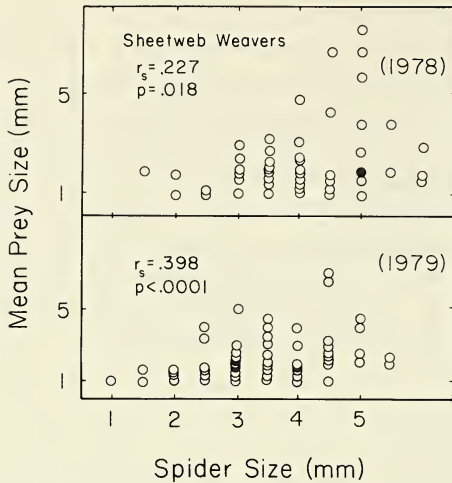


Fig. 4.—Average body length of prey in all webs of sheetweb weavers (pooled data) vs. body length of the spider. Upper graph; 1978 season. Lower graph: 1979. Black dots as in Fig. 3.

The sheetweb weaving guild showed no statistically significant relationship between body length and residence time at a website (Fig. 6) in either field season. Figure 7 shows the relationship for each species individually. Both species show similar rank correlation coefficients: $r_s = -0.072$ for *N. radiata* and $r_s = -0.079$ for *F. pyramitela*. These coefficients indicate that spider size contributes nothing to the variance in residence times for either species.

DISCUSSION

The data in Figure 1 are cumulative. However, at any one time during the growing season, the pattern shown is representative: Filmy Dome and Bowl and Doily size ranges overlap a bit, with the former being on average larger than the latter.

The size of a predator is obviously important in determining its foraging tactics (Schoener 1969, Olive 1980, 1981ab). The predator's energy requirements, ability to overcome prey and capacity for locomotion all depend to some degree on its size. The relationship between the size of a predator and its prey should be fairly straight forward: large predators tend to take larger prey than do small predators (Schoener 1971, Werner and Hall 1974, Thompson 1975). However, large predators are usually also capable of taking prey from the small end of the size spectrum.

The difference in spider size has some effect on the size of prey captured by each species. Although the guild shows a strong correlation of spider size and prey size, the two species do not have the same relationship. The reason for this is subtle. The correlation between a predator's body size and the average body size of its prey should hold for those animals that must subdue their prey by force, or for those that are limited by the size of the apparatus by which they handle their prey. For poisonous animals, the relationship between predator size and prey size will be less clear (Enders 1976), but there is still a problem with delivering the poison. The prey must be snared by the web and subdued sufficiently so that the spider can approach and bite it without risk to itself. This requirement will limit the size of prey which small spiders can handle. Thus, one could predict that the correlation between predator size and prey size should be weaker for large predators. This prediction is upheld in the case of *F. pyramitela* and *N. radiata*.

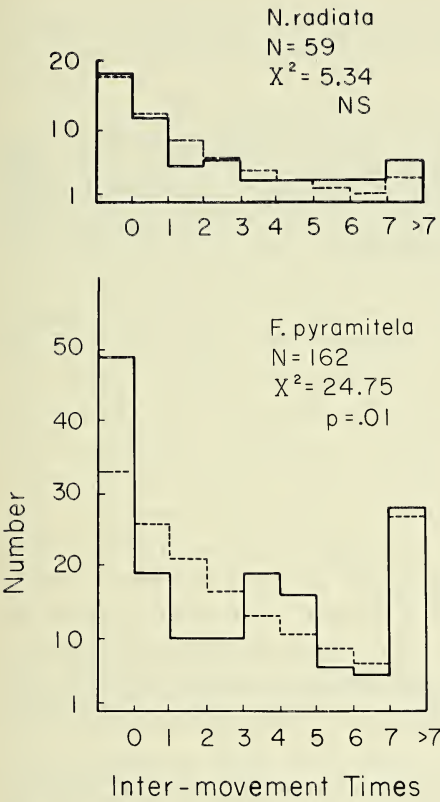
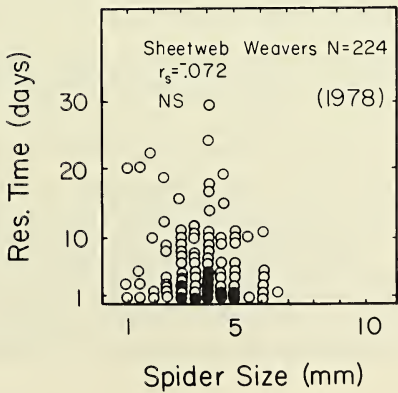
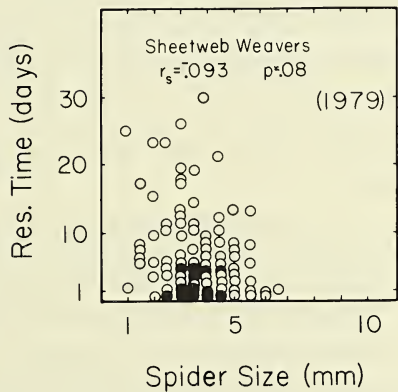


Fig. 6.—Residence times at websites vs. body length of spider for sheetweb weaving guild (pooled data). Upper graph: 1978 field season. Lower graph: 1979 field season. Spearman rank correlation is shown. Black dots as before.

Fig. 5.—Distributions of residence times (inter-movement times) at websites. Solid lines: observed distributions. Dotted lines: expected distributions from hypothesis of randomly occurring movements. χ^2 and significance levels given on graphs.



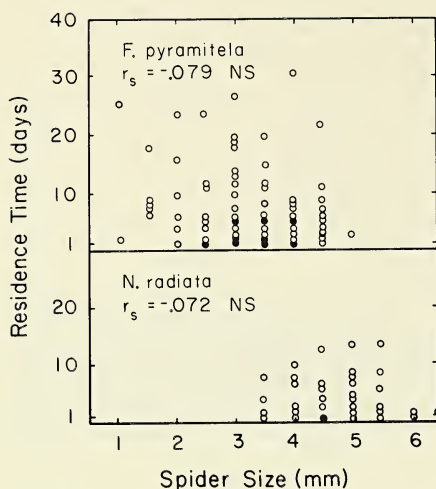


Fig. 7.—Residence times at web-sites vs. body length of spider for each species. Upper graph: *Frontinella pyramitela*. Lower graph: *Neriene radiata*. Spearman rank correlation is shown. Black dots as before.

The variation in body size also seems to have a negligible effect on the distributions of residence times at websites for the two species. There are slight differences between the two species in the average residence time at a website, but they are probably the result of differences in sample size rather than differences in biology. In both average residence time and fit to a random expectation, both species encompass nearly the entire range of variation seen in the guild as a whole; thus, the source of the variation for the guild is almost entirely intraspecific.

Wise (1975) has provided a set of field experiments bearing on the question of whether population growth of *N. radiata* is limited by the availability of food. He was able to show that adult female spiders lengthened their residence times at web-sites and increased their fecundity when their food supply was augmented. A negative effect of population density also existed such that the supply of food became a density-dependent factor.

In this study, orbweavers showed a tendency to stay at profitable websites and move quickly from sites not providing much food (Janetos 1982). Why did *F. pyramitela* and *N. radiata* not show the same trend, especially in light of Wise's (1975) study?

The answer probably lies in the different techniques used in the studies. Wise (1975) artificially enhanced food supplies at websites in order to test for food-limitation of individual fecundity and population growth rate. This study depended on the naturally occurring variation in food supply at undisturbed websites. The variation in numbers of prey captured per day and in the average size of prey at a website was less than that shown by orbweavers (Janetos 1982). Thus, the difference in results of the two studies reduces to the realization that Bowl and Doily Spiders and Filmy Dome Spiders are capable of adjusting their residence times at websites as a response to food supply, but that the variation in web site quality in my study was low enough that the behavior was not expressed. If all sites suitable for web-building are more or less equal in return rates of prey, there is little advantage in moving to a new website if the first few days at the present site are poor; a new site is unlikely to be better.

This does not necessarily mean that the linyphiids in this study were not food-limited. They may well have been. It does mean, however, that the behavioral tactic of leaving the current website in expectation of finding a "hot spot" was not adaptive, given the low variation in quality of websites. Thus, the distributions of residence times at

websites resemble those that would be expected from a hypothesis of random movements from sites, i.e. that there is a constant small probability of a stimulus to move occurring each day.

One further consequence of the relative uniformity in payoffs at websites is that there was no indication that competition for websites was important in this system. The second occupant of the site was not consistently larger than the first, as would be expected if aggressive interactions were common (Janetos 1982). In fact, in two field seasons, only one indisputable case of aggressive displacement was seen. This is in marked contrast to the case of *Agelenopsis aperta* (Riechert 1981). *A. aperta* lives in extremely harsh habitats (Riechert et al. 1973) and profitable websites in the habitat are in short supply (Riechert and Tracy 1975, Riechert 1974). Individuals battle over websites, with the larger spider usually winning (Riechert 1976, 1978). The major difference between the *A. aperta* system and this study is the number of suitable websites. The study site in New Jersey provided an abundance of possible websites. Since websites were not at a premium, one would not expect to see competitive interactions very often. The richness of the habitat makes such interactions unprofitable indeed.

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EGG GUARDING BY *CLUBIONA CAMBRIDGEI* (ARANEAE, CLUBIONIDAE) AGAINST CONSPECIFIC PREDATORS

Simon D. Pollard

Department of Zoology
University of Canterbury
Christchurch 1, New Zealand

ABSTRACT

Clubiona cambridgei is a vagrant hunting spider that oviposits in silken nests and remains with its eggs. Conspecifics were observed in the field feeding on unattended eggs, an unusual prey for a spider. In the laboratory conspecifics readily ate unattended eggs, but attended eggs were successfully guarded against predation by the resident. This implicates intraspecific egg predation as an important factor favoring maternal females that remain with their eggs. Although "egg guarding" is a label commonly applied when spiders remain with their eggs after oviposition, this is one of the few cases in which the adaptive significance of this behavior has been investigated.

INTRODUCTION

Vagrant hunting spiders commonly oviposit in silken nests and remain with their eggs. Although this behavior is often referred to as "egg guarding" (Bristowe 1958, Clyne 1979, Comstock 1940, Forster and Forster 1973, Gertsch 1949), there is surprisingly little information concerning what is meant by this term. To justify "egg guarding" as a label, the following seem necessary: to specify agents, such as predators and parasites, that constitute a threat to the eggs and to demonstrate that the female spider diminishes this threat by remaining with her eggs.

The life history of *Clubiona cambridgei* (Koch) was studied near Christchurch on the South Island of New Zealand (Pollard, in prep.). This moderately large short-sighted hunting spider (Gertsch 1949) oviposits in silken nests built in dead rolled up leaves of New Zealand flax, *Phormium tenax*. Whenever eggs were found in the field females were almost always with them. In the laboratory maternal females of this largely nocturnal species remained in their nests with their eggs day and night. However there was evidence that three egg batches found unattended in the field had been eaten: each nest was torn open, and the eggs were dry and crushed.

Little is known about the egg predators and parasites of this species. However, on one occasion a female *C. cambridgei* was observed inside a torn open nest with an egg in her chelicerae. On another occasion an inactive female was found in a nest in which all of the eggs were dry and crushed, apparently having been eaten. On yet another occasion a female was outside a nest containing another female and an egg batch. Since the female outside was bleeding from a leg wound, possibly the female inside the nest had just successfully defended her eggs.

These observations suggested a hypothesis which will be stated in two parts: *C. cambridgei* prey on the eggs of conspecifics when the opportunity arises; and by remaining with their eggs, females diminish predation on their eggs (oophagy) by conspecific spiders.

Some experiments were designed to investigate the two components of this hypothesis and some related issues (comparison of the predatory responses to eggs of maternal and non-maternal females and of males and females).

METHODS

Spiders.—Females that were collected from nests with viable eggs were referred to as “maternal.” Females that were not located in nests were referred to as “non-maternal.” Females with enlarged abdomens were presumably gravid and were not used in this study. All spiders were kept individually in cages constructed from 75 x 25 mm transparent glass vials with cotton wads providing moisture.

Handling and Testing Procedures.—A test consisted of introducing one spider, the “intruder,” into the cage with either attended or unattended eggs. No spider was used in more than one test. All tests began at 1400 hr. In tests with unattended eggs, each cage was checked at irregular intervals. After 48 hr the intruder was removed, and the nests were opened and examined for evidence of predation. In tests with attended eggs, each intruder was placed in the cage with the resident and observed for 30 min timed from initial contact with the nest. Chi square tests of independence, with Yates’ Correction, and t-tests were carried out as described by Sokal and Rohlf (1969).

Types of Tests.—1. Unattended clubionid eggs. Intruder: Non-maternal female. Twenty four nests containing females with their eggs were collected from the field on the same day as testing by cutting each flax leaf ca 1 cm to either side of the nest. Part of the folded leaf was cut away to facilitate viewing. After prodding females out of their nests, without significantly damaging the silk, the leaves were placed individually in cages. Twenty four non-maternal females were collected on the same day, and each was tested with a different unattended egg case.

2. Unattended clubionid eggs. Intruder: Maternal female. These tests were carried out as for Type 1 except in this case the maternal females removed from their nests were used as the intruders. They were collected on the same day as the test, and each was introduced to a cage with the unattended eggs of another female. Twenty maternal females were tested.

3. Unattended clubionid eggs. Intruder: Male. Except for the use of males as intruders these tests were identical to Type 1.

4. Attended clubionid eggs. Intruder: non-maternal female. The residents were 20 maternal females attending eggs they oviposited in the laboratory. The 20 intruders were each introduced singly to cages with different residents.

5. Attended clubionid eggs. Intruder: Male. Except for the use of males as intruders these were the same as Type 4.

RESULTS

Each of the 24 non-maternal females in Type 1 tests consumed all of the unattended clubionid eggs before the test ended, but none of the 20 non-maternal females in Type 4

tests ate any of the attended eggs ($X^2 = 40.059$, $P < 0.005$). In contrast to the 24 non-maternal females in Type 1 tests, none of the 20 maternal females in Type 2 tests ($X^2 = 40.059$, $P < 0.005$) and none of the 20 males in Type 3 tests ($X^2 = 40.059$, $P < 0.005$) ate unattended eggs. Also, as with females, none of the males ate attended eggs. Males walked away from the nest after contact or courted (abdomen twitching) briefly on the empty nests (Pollard and Jackson, 1982).

Each time a non-maternal female or a male contacted a nest with attended eggs, the resident became active and the intruder soon ran away. In contrast, non-maternal females rapidly entered nests with unattended eggs. Three were observed feeding on the eggs within 5 min of introduction into the cage; nine were observed feeding within 30 min; and each of the 24 had completed eating all of the eggs by the end of 16 hr. However, each remained in the nest until the 48 hr test-period had elapsed.

DISCUSSION

Egg Attendance as Guarding.—The following observations are consistent with *C. cambridgei* being important predators of the eggs of conspecifics: predation on eggs was observed in nature, unattended eggs were readily consumed in the laboratory, and this species is very abundant in nature. Since attended eggs were not eaten in the laboratory by the intruders, "guarding" seems an appropriate label for egg attendance in this species.

Spiders as Predators of Eggs.—Spiders are generally described as predators of motile insects (Clyne 1979, Comstock 1940, Forster and Forster 1973, Gertsch 1949, Main 1976, Turnbull 1973). However, there are some significant exceptions. Some lycosids scavenge on dead insects (Knost and Rovner 1975), and certain salticids have been reported feeding on the eggs of insects (Hensley 1971, Hensley et al. 1961, Jennings and Houseweart 1978, Whitcomb and Bell 1964, Whitcomb and Tadic 1963). Female spiders sometimes eat their own inviable eggs (Kaston 1965), and recently hatched spiderlings of *Achaearenea tepidariorum* (Theridiidae) have been observed feeding on sibling eggs before leaving the egg case (Valerio 1974).

Predation on eggs of conspecifics is a type of cannibalism (Fox 1975, Polis 1981). Although cannibalism is a topic often discussed with reference to spiders, predation on motile conspecifics is the type usually considered. However, the type of oophagy and cannibalism occurring in *C. cambridgei* is different from that usually associated with spiders since the eggs are not potential offspring or siblings, although similar oophagy has been reported in a web-building salticid, *Portia fimbriata* (Jackson 1982, Jackson and Blest 1982). Since the nutritive value of eggs including the yolk provided by the mother for the developing embryo would seem relatively great compared to many potential prey (Polis 1981) perhaps predation on eggs is more widespread in spiders than generally realized.

Comparison of Males and Females.—In contrast to females, males never fed on eggs of conspecifics. The males of many species of spiders and other animals seem to have a life-style that emphasizes locating, courting and mating with females, presumably at some cost to adaptations that prolong survival (Ghiselin 1974, Jackson 1978). This is probably true of *C. cambridgei* also. That the males generally responded to the nests of females in a sexual rather than a predatory fashion is consistent with this hypothesis. Also, because males are most often smaller than females (males: 8.3 ± 1.02 mm, $N = 88$; females: 9.8 ± 1.20 mm, $N = 152$; data expressed as mean $\pm$ s.d.; $t = 9.80$, $P < 0.001$), attempted predation on eggs may be more risky for them than for the non-maternal females.

Maternal Compared with Non-maternal Females.—Obviously, inhibitions against eating their own eggs are necessary in order for egg guarding by females to evolve. Since females remain with their eggs after oviposition, an ability to discriminate between their own eggs and those of other females and to prey on the latter only would not seem subject to natural selection; and the failure of maternal females to consume the eggs of other females is consistent with this. However, it is not simply that maternal *C. cambridgei* do not eat. When a sample of five females removed from their eggs were provided with *Drosophila melanogaster* on the same day, they readily captured and fed on these prey.

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CONTRIBUTION A LA CONNAISSANCE DE *CENTRUROIDES BARBUDENSIS* (POCOCK 1898) (SCORPIONES, BUTHIDAE)

Wilson R. Lourenço

Laboratoire de Zoologie (Arthropodes)
Muséum National d'Histoire Naturelle
61, rue de Buffon 75005 Paris, France

ABSTRACT

This article is a contribution to the taxonomic knowledge of *Centruroides barbudensis* (Pocock 1898). *C. barbudensis* and *C. insulanus* (Thorell 1877), previously considered as subspecies by Kraepelin (1899), are now reestablished as distinct species. *Centruroides antiguensis*, *C. hummelincki* and *C. eustatius* Armas 1976, are synonyms of *C. barbudensis*. Data are added on the distribution and the ecology of *C. barbudensis*.

RESUME

Cette note est une contribution à la connaissance de *Centruroides barbudensis* (Pocock 1898). *C. barbudensis* et *C. insulanus* (Thorell 1877), considérées comme sous-espèces par Kraepelin (1899), sont à présent rétablies au rang spécifique. *Centruroides antiguensis*, *C. hummelincki* et *C. eustatius* Armas, 1976 sont synonymes de *C. barbudensis*. Des nouvelles données sont apportées sur la répartition et l'écologie de *C. barbudensis*.

INTRODUCTION

Avec la présente note, nous débutons une série d'études qui sera réalisée sur la faune des Scorpions des Antilles françaises.

La faune en question est représentée par deux familles, celle des Buthidae et celle des Diplocentridae. Les Diplocentridae, représentés par *Oiechus purvesii*, *Didymocentrus lesueurii* et *Heteronebo vachoni*, ont déjà fait l'objet d'importantes études, réalisées par Francke (1978) dans son travail monographique sur les Diplocentridae de la région antillaise. La famille des Buthidae, moins étudiée jusqu'à présent, est représentée aux Antilles françaises (dans l'état actuel de nos connaissances), par deux genres: *Isometrus*, avec l'espèce "cosmopolite" *I. maculatus* (Vachon 1972, Armas 1976a) et *Centruroides*, pour lequel deux formes ont été observées. La première assez courante en Guadeloupe, mais également retrouvée dans les îles des Saintes, Maria Galante et Desirade, est actuellement le sujet des études de nos collègues américains O. F. Francke et W. D. Sissom (comm. in litt, 1981); elle correspond à une espèce nouvelle et sera décrite dans un travail prochain des chercheurs cités. La deuxième forme, retrouvée particulièrement dans l'île Fourchue, située entre Saint-Martin et Saint-Barthélemy, mais également sur ces deux dernières îles, et aussi en Guadeloupe et Martinique, fut déterminée par nous comme *Centruroides barbudensis* (Pocock 1898), espèce décrite de Barbuda et de Bird's island.



1



2



3



4

Figs. 1-4.— *Centruroides barbudensis*: 1 et 2, mâle, vues dorsale et ventrale; 3 et 4, femelle, vues dorsale et ventrale.

Dans la présente note nous redécrivons *C. barbudensis*, et une analyse critique est proposée sur les espèces proches, souvent confondues avec cette dernière: *Centruroides insulanus* (Thorell 1877), *Centruroides antiguensis*, *Centruroides hummelincki* et *Centruroides eustatius* décrites par Armas (1976b).

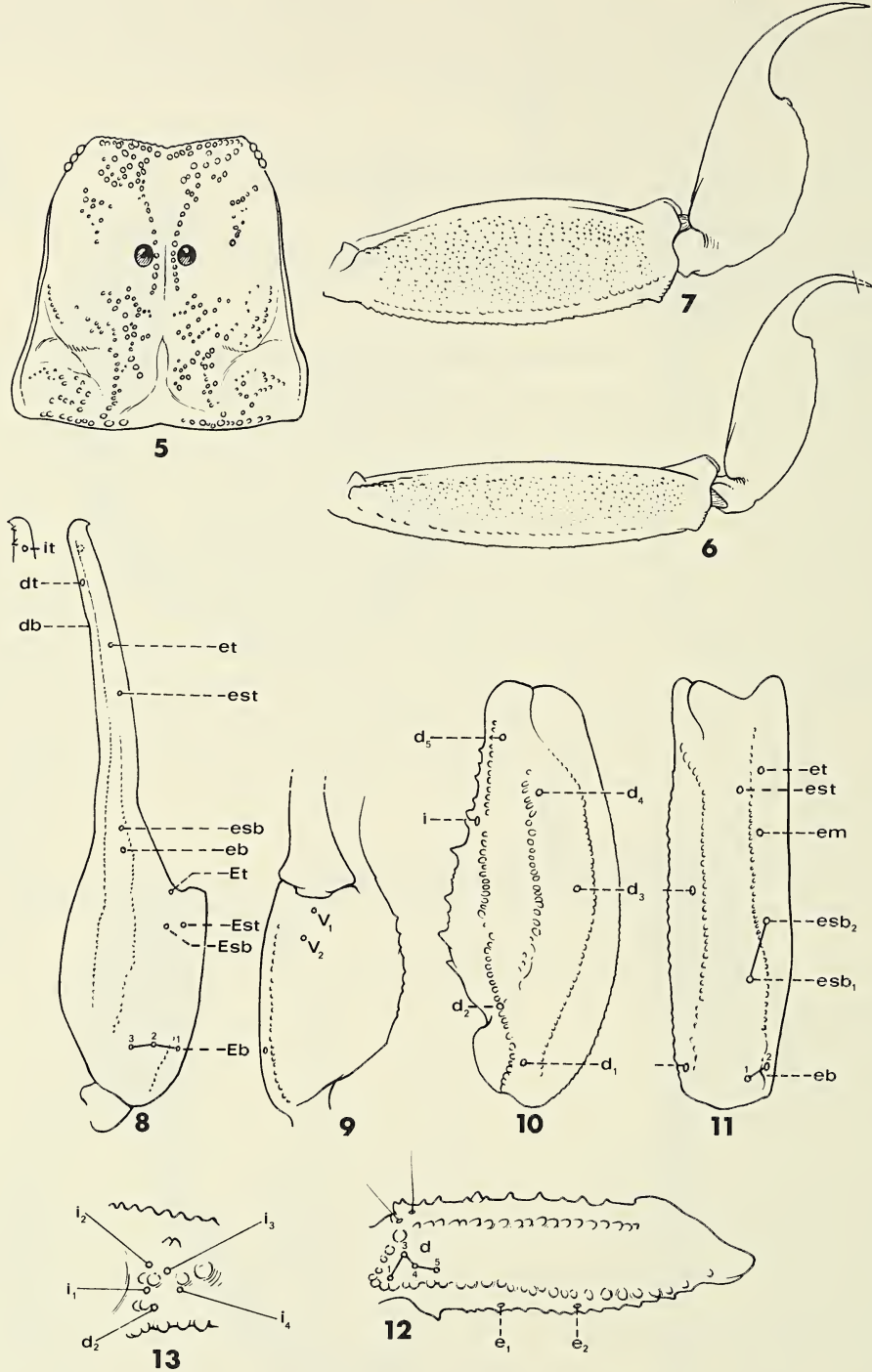
Centruroides barbudensis (Pocock)

Centrurus barbudensis Pocock 1898:386.
Centrurus insulanus barbudensis: Kraepelin 1899:91; Stahnke et Calos 1977:118.
Rhopalurus testaceus barbudensis: Meise 1934:32.
Centruroides barbudensis: Armas 1976:53.

Mâle.—(Figs. 1 et 2), MNHN-RS-3026, Ile Fourchue, R. Pinchon leg., 19/IV/1954.
Coloration général jaunâtre, avec des taches brunâtres. Prosoma: plaque prosomienne jaunâtre avec des taches brunâtres, situées dans la région antérieure et à l'arrière du tubercule oculaire, au long des carènes médianes postérieures; les bords latéraux sont peu pigmentés. Tubercule oculaire et yeux latéraux noirs. Mesosoma: tergites jaunâtres, avec la présence de deux taches longitudinales brunâtres qui sont la continuité des taches postérieures de la plaque prosomienne; septième tergite avec les taches moins marquées que sur les six précédents; quelques esquisses de taches présentes sur la carène axiale, et sur les bords latéraux des tergites. Metasoma: anneaux I à V et vésicule jaunâtres; présence de quelques esquisses de taches au long des carènes ventrales, en particulier des anneaux I à IV; aiguillon à base jaunâtre et à extrémité rougeâtre. Sternites jaunâtre foncé. Peignes, opercule-génital, sternum, hanches et processus maxillaires ocre-jaune. Pattes jaunâtres avec de nombreuses taches brun-clair, diffuses, qui forment une espèce de réticule. Chélicères jaunâtres avec un réticule de taches brunâtres; les doigts sont jaune-rougeâtre.

Tableau 1.—Mensurations (en mm) des exemplaires décrits.

	Mâle	Femelle
Longueur totale	62,6	52,5
Prosoma, longueur	4,6	5,1
Prosoma, largeur antérieure	3,2	3,7
Prosoma, largeur postérieure	4,9	5,5
Mesosoma, longueur totale	14,0	13,4
Metasoma, longueur totale	44,0	34,0
Anneau caudal I, longueur/largeur	5,9/2,2	4,6/2,9
Anneau caudal II, longueur/largeur	7,4/2,0	5,2/2,7
Anneau caudal III, longueur/largeur	7,9/2,0	5,6/2,6
Anneau caudal IV, longueur/largeur	7,9/2,0	5,7/2,5
Anneau caudal V, longueur/largeur/hauteur	8,6/2,0/2,0	6,5/2,5/2,4
Telson, longueur	6,3	6,4
Vésicule, longueur/largeur/hauteur	4,4/2,0/1,9	4,0/2,1/2,0
Aiguillon, longueur	1,9	2,4
Pédipalpe, longueur totale	22,2	21,5
Fémur, longueur/largeur	5,5/1,4	5,1/1,5
Tibia, longueur/largeur	6,1/1,9	5,9/2,2
Pince, longueur/largeur/hauteur	10,6/2,2/2,0	10,5/2,5/2,1
Doigt mobile, longueur	6,3	6,9



Figs. 5-13.—*Centruroides barbudensis*: 5, plaque prosomienne (femelle); 6 et 7, Cinquième anneau et vésicule, vue latérale (mâle et femelle); 8-13, Trichobothriotaxie (femelle) - 8, pince, vue externe; 9, pince, vue ventrale; 10, tibia, vue dorsale; 11, tibia, vue externe; 12, fémur, vue dorsale; 13, fémur, vue interne, détail.

Tableau 2.—Variations du nombre des dents des peignes chez *C. Barbudensis*.

Nombre des dents	Mâles	Femelles	Immatures
18	—	7	--
19	2	27	—
20	4	16	8
21	—	4	9
22	2	--	5

Morphologie. Prosoma: front de la plaque prosomienne avec une concavité peu importante; tubercule oculaire antérieur par rapport au centre de la plaque prosomienne; yeux médians séparés par plus d'un diamètre oculaire; trois paires d'yeux latéraux. Carènes du prosoma (Vachon 1952): carènes médianes oculaires formant un sillon interoculaire bien marqué; carènes latérales oculaires commençant après le bord dorsal des yeux latéraux et se poursuivant en direction des yeux médian sur une distance d'un peu plus d'un tiers de celle comprise entre les yeux latéraux et les yeux médians; carènes médianes postérieures délimitant approximativement un carré dans la région postéro-médiane de la plaque prosomienne; la plaque prosomienne est bien granulée, avec des granules moyens (Fig. 5). Mesosoma: tergites moyennement granulés; les granules plus importants sont disposés sur les taches longitudinales. Carène axial bien marquée sur tous les tergites. Tergite VII avec cinq carènes bien marquées: une axiale incomplète dans la région postérieure, deux médianes et deux latérales complètes. Metasoma: anneau I avec 10 carènes; anneau II, III et IV avec 8 carènes; anneau V avec 5 carènes; espaces intercarénaux très peu granulés. Cinquième anneau arronid, avec les carènes très peu marquées. Vésicule piriforme, aplatie, allongée, lisse; aiguillon assez court par rapport à la vésicule; épine sous-aiguillonnaire très réduite, rhomboïde (Fig. 6). Sternites à stigmates aplatis, linéaires. Peignes avec 20-20 dents (type-mâle avec 22-22, bien que Pocock cite 23). Pédipalpe: fémur avec 5 carènes complètes; tibia avec 7 carènes complètes et une carène interne-dorsale à granules mieux différenciés, spinoformes; 9 carènes sur la pince, moyennement marquées, 4 se prolongent sur le doigt fixe; carène interne-dorsale, présentant également quelques granules spiniformes. Tranchant des doigts mobiles avec 8-8 séries de granules; lobe basilaire moyennement développé. Chélicères avec la dentition caractéristique des Buthidae (Vachon 1963); doigt fixe avec une seule dent interne; doigt mobile avec deux dents basales. Trichobothriotaxie: les figures 8 à 13 précisent le nombre et la disposition des trichobothries des pédipalpes. Les caractères à souligner sont: (a) présence de 5 trichobothries à la base du fémur, face interne, par suite de l'émigration sur cette face de la trichobothrie dorsale d_2 ; (b) trichobothries dt et db toutes deux distales de et ; (c) les deux trichobothries et et em de la face externe du tibia sont toujours situées du même côté de la carène externe de cet article; (d) les trichobothries dorsales d_3 et d_4 du tibia sont toutes deux situées du même côté de la carène médiane dorsale; (e) les deux trichobothries externes du fémur e_1 et e_2 sont toutes deux distales de d_5 ; (f) les trichobothries esh , Esb , Eb_3 et d_2 sont de petites trichobothries à arèle petite et soie courte.

Femelle.—(Figs. 3 et 4), MNHN-RS-3026, Ile Fourchue, R. Pinchon leg., 19/VI/1954 (seules les différences par rapport au mâle sont signalées).

Coloration, semblable à celle du mâle, cependant les taches sont plus marquées, particulièrement sur les pédipalpes, sur les pattes et dans la région ventrale du metasoma. Morphologie. Les anneaux de la queue sont plus courts et plus larges que ceux du mâle; la vésicule est plus ovale et l'aiguillon est proportionnellement plus long (Fig. 7). Les

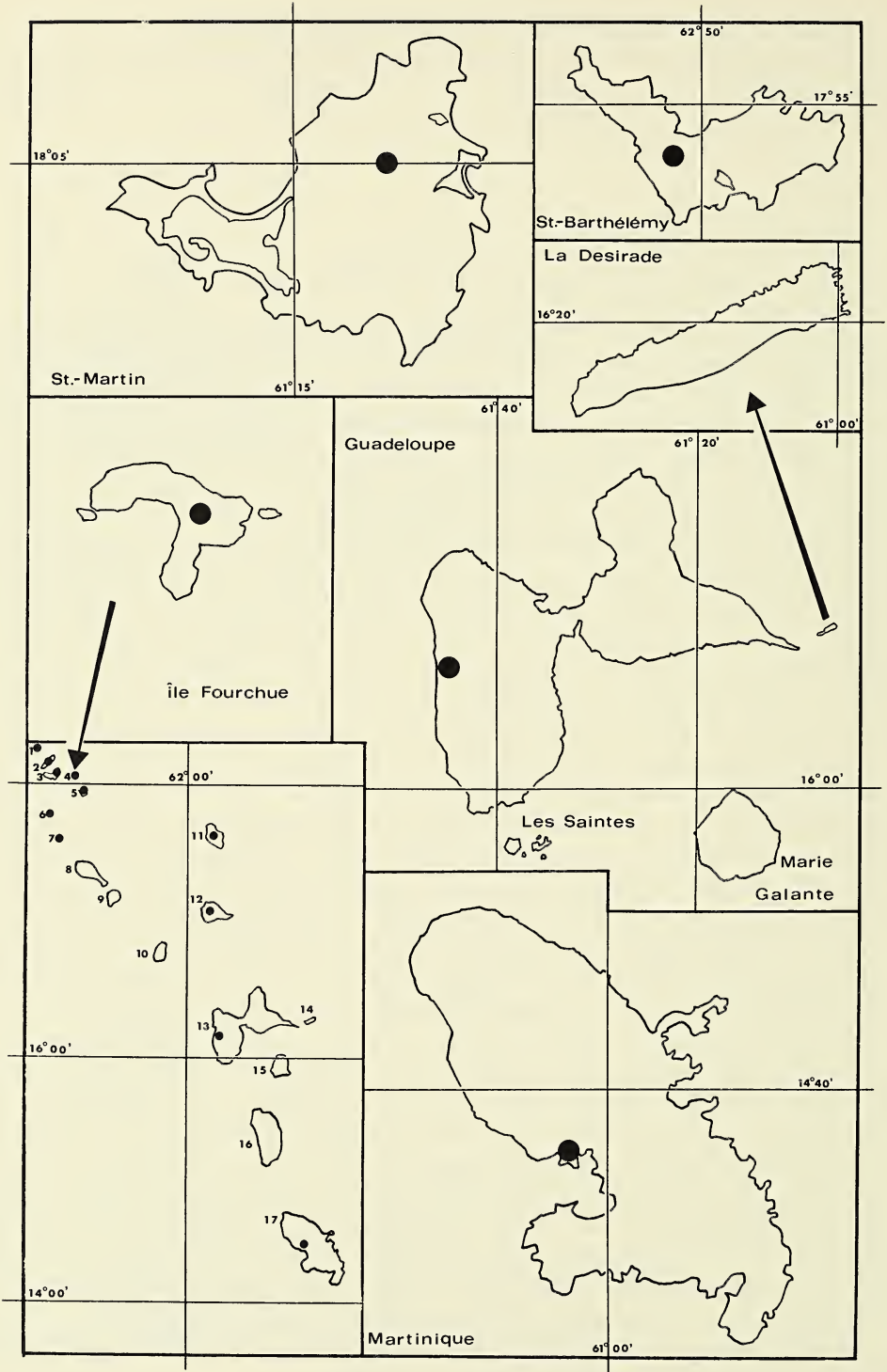


Fig. 14.—Répartition de *Centruroides barbudensis*. Sigles: 1 = Sombbrero, 2 = Anguilla, 3 = St.-Martin, 4 = île Fourchue, 5 = St-Barthélémy, 6 = Saba, 7 = St.-Eustatius, 8 = St. Kitts, 9 = Nevis, 10 = Montserrat, 11 = Barbuda, 12 = Antigua, 13 = Guadeloupe, 14 = Desirade, 15 = M. Galante, 16 = Dominique, 17 = Martinique.

Tableau 3.—Formules globales du nombre des dents des peignes chez *C. barbudensis*.

Formule globale	Mâles	Femelles	Immatures
18-18	—	1	—
18-19	—	3	—
19-18	—	1	—
19-19	—	10	—
20-19	—	1	—
19-20	1	2	—
20-19	1	1	—
20-20	1	5	3
20-21	—	1	2
21-20	—	1	—
21-21	—	1	3
21-22	—	—	1
22-22	1	—	2

carènes du metasoma et des pédipalpes sont plus marquées. Lobe basilaire des doigts mobiles des pédipalpes plus réduits; 8-8 séries de granules sur le tranchant. Peignes plus petits avec 19-19 dents.

Materiel Etudie.—*Centruroides antiguensis*. Anguilla, juillet 1949 (A. MacDonald), 1 femelle (RU). Antigua, near Bats cave E of Nelson’s Dockyard (sta. 591), 13 juillet 1955 (P. W. Hummelinck), 1 femelle (holotype) (RU). Barbuda, Martello tower (in wood-shed at light, sta. 596), 8 juillet 1955 (P. W. Hummelinck), 1 mâle, 1 femelle (RU).

Centruroides barbudensis. Barbuda (Leeward Is., W. Indies) (W. R. Forrest), 1 mâle (lectotype, H. L. Stahnke) (BMNH). Guadeloupe, Bouillante: hôte du village, 16 novembre 1977 (F. Chalumeau), 1 femelle (MNHN). Saint-Martin, Pic du Paradis (470 m alt., sous-écorce), 19 septembre 1976 (F. Chalumeau), 1 femelle, 11 immatures (MNHN). Martinique, Fort de France, 12 mars 1953 (R. Pinchon), , 2 femelles (MNHN). Ile Fourchue (sous des pierres), 19 avril 1954 (R. Pinchon), 3 mâles, 23 femelles (MNHN).

Centruroides eustatius. St. Eustatius, Quill, Glass Bottle (sta. 431A), 12 juillet 1949 (P. W. Hummelinck), 1 femelle (holotype), 2 immatures (RU).

Centruroides hummelincki. Saba, 6 mars 1962 (J. J. Beaujon), 1 femelle (holotype) (RU). Saba, Botton, 20 juillet 1949 (P. W. Hummelinck), 1 femelle (paratype) (RU).

Centruroides insulanus. Jamaïque (Stuxberg), 1 mâle, 1 femelle, 1 immature (NRS).

REMARQUES TAXONOMIQUES

L’examen de trois exemplaires de *Centruroides insulanus* (Thorell 1877), de la collection Thorell (non types), nous a permis de constater que cette espèce est assez différente de *C. barbudensis*; les différences sont particulièrement importantes entre les mâles des deux espèces, *C. barbudensis* ayant une queue bien plus longue et plus fine que celle de *C. insulanus*; la vésicule de *C. barbudensis* est piriforme tandis que celle de *C. insulanus* est bien plus ovale (Pocock 1898). Les deux espèces présentent les bandes foncées longitudinales sur le dos, cependant la distribution des pigments sur l’ensemble du corps et des segments est bien différente. La décision de Kraepelin (1899) de considérer *C. barbudensis* comme sous-espèce de *C. insulanus* ne nous paraît pas justifiée, *C barbudensis* devant être conservé au niveau spécifique.

Armas (1976b) décrit trois espèces de *Centruroides* pour les petites Antilles: *C. antiguensis*, d’Antigua, *C. hummelincki* de Saba et *C. eustatius* de St. Eustatius. Il signale dans ses très brèves descriptions que les trois espèces sont assez proches de *C. barbudensis*.

Armas (in litt., 1981) nous communique que *C. eustatius* est un synonyme de *C. barbudensis*, et que *C. antiguensis* passerait au rang de sous-espèce de *C. barbudensis*, comme *C. b. antiguensis*. L'étude des types des trois espèces citées, nous a permis de conclure qu'elles sont toutes les trois synonymes de *C. barbudensis*. Les petites différences indiquées par Armas (1976b) sont dues à des variations intra-spécifiques. De plus, les stations typiques de ces trois espèces: Antiqua, Saba et St. Eustatius sont à l'intérieur même de l'aire de distribution connue de *C. barbudensis*.

REMARQUES ECOLOGIQUES ET BIOGEOGRAPHIQUES

Centruroides barbudensis a été décrit par Pocock (1898) qui donne comme station type, Barbuda et Bird's island. Armas (in litt., 1981), nous a communiqué avoir examiné des exemplaires de cette espèce, provenant de St. Eustatius, St. Martin, Anguilla et Sombbrero.

D'après le matériel que nous avons étudié, appartenant à *C. barbudensis*, nous pouvons affirmer que cette espèce se retrouve particulièrement dans l'Ile Fourchue, où elle semble assez abondante, mais aussi à St. Martin, en Guadeloupe et en Martinique. R. Pinchon qui a récolté la plupart des exemplaires, affirme dans les lettres accompagnant le matériel envoyé au Muséum qu'il l'a retrouvée à Saint Barthélemy également.

Dans l'Ile Fourchue, *C. barbudensis* a été retrouvé sous des pierres, le nombre des biotopes possibles pour les Scorpions devant être restreint sur cet îlot. A Saint-Martin il fut récolté sous des écorces; en Guadeloupe, le seul exemplaire trouvé, fut vraisemblablement récolté sous des écorces; la région de Bouillante, située en Basse-Terre, présente une végétation du type forêt sèche (Fournet 1981); la pluviosité moyenne annuelle de cette région, est la plus réduite de toute la Basse-Terre, étant inférieur à 1200 mm (Corre 1981). Pour les exemplaires capturés en Martinique, nous ne disposons à l'heure actuelle d'aucune donnée écologique (Fig. 14).

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MAINTENANCE FEEDING OF FIRST INSTAR MANTISPID LARVAE (NEUROPTERA, MANTISPIDAE) ON SPIDER (ARACHNIDA, ARANEAE) HEMOLYMPH

Kurt E. Redborg¹ and Ellis G. MacLeod

Department of Entomology
University of Illinois
Urbana, Illinois 61801

ABSTRACT

After measuring their initial weights, we induced first instar larvae of *Mantispa uhleri* Banks to board individual *Salticus scenicus* (Clerck) adults and immatures. After varying periods of time (2 to 73 days), larvae were removed from their spiders and reweighed. Changes in larval weight were analyzed by multiple linear regression. Results demonstrate that larvae increase in weight in proportion to their tenure on a spider. Because of this we suggest that larvae are maintaining themselves by feeding on spider blood. The significance of initial weight in accounting for variation in weight change suggests that there may be an optimal maintenance weight range for larvae while on a spider.

INTRODUCTION

Members of the neuropteran family Mantispidae (subfamily Mantispinae) have often been categorized as "parasites in the egg sacs of spiders." This alludes to their complex life cycles in which larvae enter spider egg cases and feed on the eggs within by piercing them and draining their contents. First instar mantispids, depending on species, can locate spider eggs by two different routes: the direct penetration of an egg sac already spun, or the boarding of a female spider prior to egg production with entering of the egg sac at the time of its construction (Redborg and MacLeod 1983). Whichever method is utilized, this feeding ecology is inappropriately termed parasitism; mantispids are actually spider egg predators.

Mantispa uhleri Banks is an unexpectedly common species in Illinois and surrounding states. Larvae of this mantispid will facultatively use either of the above mentioned egg location strategies, although data indicate that it is predominantly a spider boarder. Larvae will climb aboard a wide variety of hunting spiders and adopt position preferentially on the spider's pedicel (Redborg and MacLeod 1983). In awaiting the production of eggs, larvae will enter the book lungs of immature spiders when a spider molt occurs. Larvae may remain aboard a spider for several months. In fact, this insect overwinters in Illinois as a first instar on its spider host. We present data that show that this mantispid maintains itself during its tenure on a spider by feeding on spider blood. In this respect, *M. uhleri* does indeed turn out to be a true spider parasite.

¹Present address: Department of Physiology and Biophysics, University of Illinois, 407 South Goodwin Avenue, Urbana, IL 61801.

MATERIALS AND METHODS

Our intent was to measure significant weight increases of larvae on boarded spiders which could be attributable to larval feeding. First instar *M. uhleri* were obtained from laboratory culture using methods described in detail elsewhere (Redborg and MacLeod 1983). For the spider to be boarded we chose the small salticid *Salticus scenicus* (Clerck). Spiders were readily collected on the walls of buildings in the Urbana, Illinois area during the months of April and May. A total of 63 spiders (22 immatures, 10 males, 31 females) were utilized in the experiment. Each spider was confined for a 24 hr period in a cotton-stoppered 2-dram shell vial with one first instar *M. uhleri*. Prior to confinement, each larva was anesthetized with CO₂ and weighed on a Cahn Electrobalance. A calibration series of larvae indicated that most initial weights would fall in the 2-6 μg range. Repeated weighings of short lengths of #46 copper wire estimated the standard error of our measurements as approximately $\pm 0.5 \mu\text{g}$ (95% confidence interval).

Larvae had invariably crawled aboard the spider within the 24 hr period. Each spider was then transferred to a ventilated plastic cage (8.5 x 12.5 x 6.0 cm), containing a small culture of *Drosophila melanogaster* Meigen and a water supply, and maintained at 25° C at a photoperiod of L:D = 16:8. After varying periods of time (2 to 73 days) larvae were randomly removed from spiders under CO₂ anesthesia and immediately reweighed. To remove any possible bias in measuring larval weights, larvae were selected and removed from the spider by one of us while the other did the reweighing. In this way the person taking a larva's second weight had no knowledge of the initial reading.

Data were analyzed by a step-wise multiple regression procedure. Larval weight change (positive or negative) was the designated dependent variable. Initial larval weight and number of days (D) a larva was on a spider were independent variables. Days squared (D x D) and days cubed (D x D x D) were also included as variables to test for any significant curvilinear trends.

RESULTS

Most of the larvae (57 of 63) adopted positions around the spider's pedicel, and the other six were found under the edge of the carapace or around the base of one of the legs. Initial larval weights ranged from 2.6 to 7.6 μg with a mean of 4.6. The mean weight change for all larvae was +0.481 μg . Many larvae showed weight gains which, on the basis of the estimated standard error of our weighings, could be considered significant. However, other larvae showed significant weight losses. This anomaly can be put into perspective by examination of Table 1 which contains results of the regression analysis showing that initial larval weight had a surprising influence on weight change. Larvae with low initial weights were more often associated with positive weight gains while heavier larvae often showed weight decreases.

The most significant variable accounting for variation in larval weight change was the number of days on a spider; this variable entered the regression equation first, followed by the variable of initial larval weight. Days squared, days cubed, and the interaction of days and initial weight were all insignificant ($P > 0.05$) and did not enter the equation. The final equation ($y = 0.0537x_1 - 0.845x_2 + 3.205$; y = larval weight change; x_1 = days on spider; x_2 = initial larval weight) was highly significant (Table 2) accounting for 45% of the variation in larval weight change. Figure 1 depicts the partial regression line through the data points with initial weight held constant at its mean value of 4.6 μg .

Table 1.—Regression coefficients and levels of significance for variables in step-wise regression analysis of larval weight change data.

Variable	Partial Regression Coefficient	F	Significance
..... in equation			
Days on spider	0.0537	30.027	P < 0.001
Initial larval weight	-0.845	21.404	P < 0.001
(Constant)	3.205		
..... not in equation			
Days squared (D x D)	--	2.842	P = 0.097
Days cubed (D x D x D)	--	2.558	P = 0.115
Interaction	--	0.110	P = 0.741

DISCUSSION

Very early in our laboratory work with *M. uhleri* it became virtually certain, for several circumstantial reasons, that first instar larvae that had boarded various species of spider, e.g. *Phidippus audax* (Hentz) and *Lycosa rabida* Walckenaer, were feeding on spider blood. Larvae usually positioned themselves on the spider at locations (pedicel after first boarding; book lung after spider ecdysis) covered by thin, membranous cuticle that it would seem could be easily penetrated by a larva's mouthparts. Discolored patches, similar to those described for wound repair in *Geolycosa pikei* (Marx) (Bursey 1981), were often evident on the spider's integument near the larva's mouthparts after a larva had been aboard a spider for several weeks. After this amount of time, a darkened area could also be observed in the larva's midgut, suggesting that some material had been ingested. Such midgut coloration is always evident in wild-caught larvae removed from spiders. Another indication that larvae were feeding is the admittedly subjective observation that larvae removed from spiders appeared "plumper" than their newly-hatched counterparts.

The significant partial regression coefficient (Table 1) for the variable of days on a spider objectively demonstrates that larvae increased in weight in proportion to their length of tenure on a spider. Although there are other possible explanations for this phenomenon, such as absorption of atmospheric water, we feel the most reasonable, in light of the above observations, to be maintenance feeding on spider hemolymph. Although we have not recorded *S. scenicus* as a natural host for *M. uhleri*, we have no hesitation in extrapolating these data to other species of spider. *Mantispa uhleri*'s host range is extremely broad and encompasses nearly all of the families of hunting spiders (Redborg and MacLeod 1983). We think it likely that natural larval behavior will be exhibited on any hunting species. In support of this we relate that several female *Salticus* bearing larvae were allowed to spin egg sacs. Larvae successfully entered these sacs and produced normal, albeit extremely small, adults.

The negative intercept of the partial regression line in Figure 1 indicates that an average larva (4.6 μ g initial weight) at first loses weight before ultimately showing a positive weight gain. Intuitively, a line representing this relationship must begin at the origin, since weight change by definition at day zero is zero, dip below the x-axis, and then show a positive slope. However, we have chosen to represent the relationship as a

Table 2.—Analysis of variance for multiple regression equation $y = 0.0537x_1 - 0.845x_2 + 3.205$; y = weight change of larva; x_1 = days on spider; x_2 = initial weight of larva. $r^2 = 0.448$.

Source of Variation	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	Significance
Regression	2	85.729	42.864	24.381	$P < 0.001$
Residual	60	105.488	1.758		

straight line since the variables (days squared and days cubed) that would have produced a curvilinear equation were not significant (Table 1). There are two likely reasons for this lack of significance. First, larvae might have lost weight slowly over a period of several days or weeks while they were positioning themselves on the spider in preparation for feeding. Then, weight might have been regained slowly after feeding commenced. We may simply have collected too few data points during this critical period to adequately document this trend. The second, and we feel more probable, explanation is that weight loss occurred rapidly while larvae were searching the vial and before boarding of the spider had even taken place. Under this circumstance it would have been impossible for us to detect this rapid change since it would have already occurred before larvae could be removed from a spider and reweighed.

Since larvae do not engorge while aboard a spider, the line in Figure 1 must also eventually level off since there is obviously a limit to weight gain. More data points in the

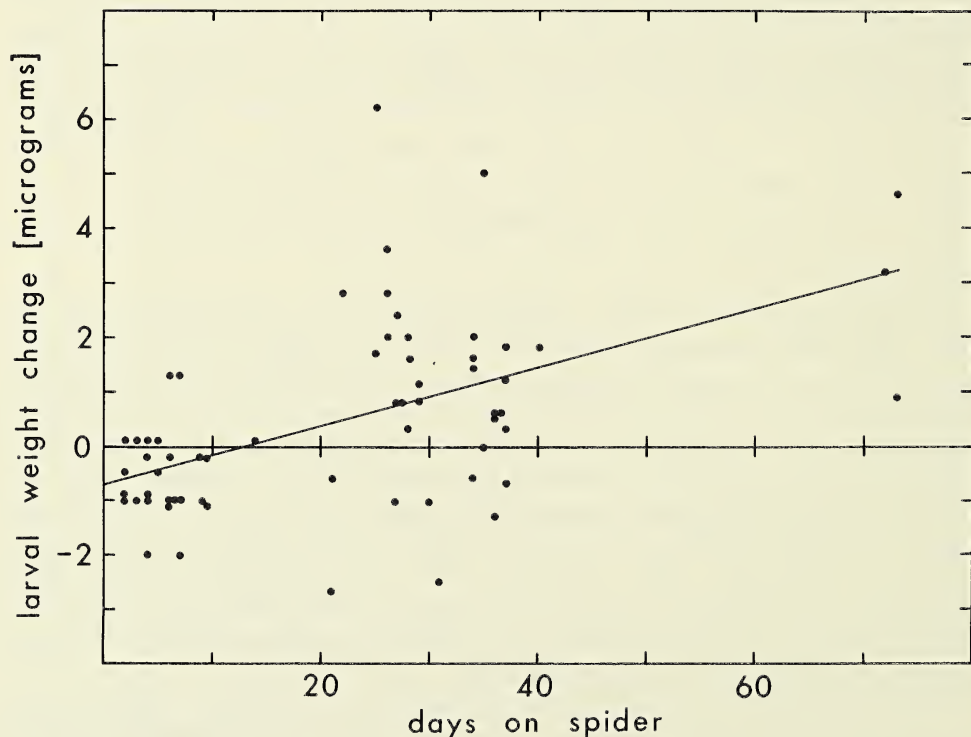


Fig. 1.—Partial regression of larval weight change (μg) versus the number of days each larva was aboard a spider. Equation of line: $y = 0.0537x_1 - 0.845x_2 + 3.205$ with x_2 held constant at its mean value of $4.6 \mu g$; y = larval weight change; x_1 = days on spider; x_2 = initial larval weight.

50-100 day range would likely have shown this statistically (days squared was approaching significance at $P = 0.097$ even with our available data).

The significance of initial larval weight (Table 1) in accounting for weight change was surprisingly and totally unexpected. This suggests that there is some optimal maintenance weight range which larvae gravitate toward while on a spider. Heavy larvae may actually refrain from feeding initially and decrease in weight to reach this range before eventually feeding to maintain it.

Larvae may spend up to one year on a spider before reaching an egg sac (Redborg and MacLeod 1983) and the nutritional reinforcement provided by spider blood very likely helps them survive this period. This trophic association, separate and apart from eventual predation on spider eggs, is an example of true parasitism. This term has been used inappropriately in the past to describe mantispid-spider associations, but ironically turns out to be correct for describing the spider-inhabiting portion of *M. uhleri*'s life cycle.

Perhaps the most intriguing aspect of these data is the potential they establish for chemical communication between mantispid and spider. Larvae of *M. uhleri* are capable of determining when the spider they have boarded becomes an adult female (Redborg and MacLeod 1983) and this ability may be partly facilitated by hormonal or other chemical cues in ingested spider blood. In a similar fashion, a larva might be alerted by chemical signals to impending oviposition. Recent evidence (Redborg 1982) has documented alterations in the development of *Lycosa rabida* induced by the boarding and subsequent parasitic feeding of *M. uhleri*. Parasitized female spiders matured one instar earlier than nonparasitized controls while no such alterations occurred in male spiders. Several explanations were advanced for this sex-specific response, including the injection of some substance into the spider by the feeding mantispid. More details of the coevolutionary relationships between spiders and *M. uhleri* are obviously needed. We hope that the results reported here will serve as a foundation for future investigations.

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DESCRIPCION DE *WEDOQUELLA* NUEVO GENERO (ARANEAE, SALTICIDAE)

María Elena Galiano

Investigador del CONICET
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"
Av. Angel Gallardo 470, 1405 Buenos Aires, R. Argentina

ABSTRACT

Wedoquella new genus is described. Closest to *Phiale* by its general appearance and quetotaxy, it differs in having two retrolateral apophyses on the palpal tibia and in the structure of the epigynum. Two new species from Argentina, *W. denticulata* (type-species of the genus) and *W. macrothecata* are described based on specimens reared in the laboratory. *Evophrys* (?) *punctata* Tullgren, 1905 from Bolivia is transferred to *Wedoquella*, the male is described for the first time and the species is newly recorded from Argentina. *Pensacola variegata* Mello-Leitão, 1939 is newly synonymized with *W. punctata*. Females of *W. denticulata* and *W. punctata* have two color variants.

EXTRACTO

Se describe *Wedoquella* nuevo género. Próximo a *Phiale* por su aspecto general y quetotaxia, se diferencia por tener dos apófisis retrolaterales en la tibia del palpo y por la estructura del epigino. Se describen dos nuevas especies de la Argentina, *W. denticulata* (especie tipo del género) y *W. macrothecata*, basándose en especímenes criados en el laboratorio. *Evophrys* (?) *punctata* Tullgren, 1905 es transferida a *Wedoquella*, el macho se describe por primera vez y se la cita como nueva para la Argentina. *Pensacola variegata* Mello-Leitão, 1939 se sinonimiza con *W. punctata*. Las hembras de dos de las especies, *W. denticulata* y *W. punctata* tienen dos variantes de color.

INTRODUCCION

Las tres especies que integran *Wedoquella* nuevo género, han estado en estudio por casi veinte años. El aspecto general, el colorido y la quetotaxia son muy similares a los de *Phiale tristis* Mello-Leitão, 1945 y durante cierto tiempo, se pensó que se trataba de otras especies de *Phiale*. El hecho de que *Wedoquella punctata* (Tullgren, 1905) n. comb., fuera ubicada por el autor en *Evophrys* con un interrogante y descripta como *Pensacola variegata* por Mello-Leitão (1939) demuestra la ambigüedad de las definiciones de algunos géneros del grupo de salticidas unidentadas.

Delimitados los caracteres de *Phiale* por el estudio del holotipo hembra y de los ejemplares machos (Galiano 1978, 1981a, 1981b) se hizo evidente que las especies en cuestión pertenecían a un género diferente de los conocidos.

Machos y hembras de *W. punctata* son fácilmente identificables debido a un patrón de diseño y colorido característico y similar en ambos sexos. En cambio *W. macrothecata*

n. sp. y *W. denticulata* n. sp. presentan semejantes patrones con muy escasas variantes por lo que la asignación de machos y hembras a cada una de las especies solo pudo hacerse correctamente cuando a partir de 1978 comenzaron a criarse en el laboratorio. Pese al tamaño relativamente reducido de las arañas en el momento de abandonar el cocoon, demostraron una buena adaptabilidad a las condiciones del bioterio y se obtuvieron adultos.

Las especies de *Wedoquella* se hallan en áreas subtropicales selváticas de Bolivia, Paraguay y norte de la Argentina. En el Parque Nacional Iguazú comparten el habitat con *Phiale gratiosa* y *P. tristis*. En octubre y noviembre se encuentran adultos de ambos sexos, las hembras generalmente ya fecundadas. El nido es discoidal, de seda blanca, con dos aberturas opuestas. La hembra permanece encerrada con el cocoon hasta que se dispersan las crías. Los juveniles de *W. macrothecata* y *W. denticulata* son amarillo pálido, con los ojos en manchas negras; las hileras, dos manchitas apicales ventrales y dos líneas paralelas dorsales en el opistosoma, negros. En el bioterio se los alimentó con *Drosophila* y *Musca domestica*. A fines de marzo algunos machos alcanzan ya la madurez, mientras que las hembras realizan la última muda entre setiembre y diciembre.

Los especímenes estudiados se encuentran depositados en el Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Museum of Comparative Zoology, Harvard (MCZ), Naturhistoriska Riksmuseet, Stockholm (NRS), Muséum d'Histoire Naturelle de Bâle (MHNB) y colección M. E. Galiano (MEG). Las medidas se expresan en milímetros y se tomaron según métodos explicados en una publicación anterior (Galiano 1963). La quetotaxia se menciona según sistema de Platnick y Shadab (1975). Las abreviaturas son: p = prolateral, r = retrolateral, v = ventral, OMA, OLA, OMP y OLP ojos medios anteriores, laterales anteriores, medios posteriores y laterales posteriores, respectivamente.

Wedoquella, nuevo género

Especie tipo.—*Wedoquella denticulata*, nueva especie.

Etimología.—El nombre genérico es una combinación arbitraria de letras más el sufijo latino diminutivo *-ella* y se considera femenino.

Diagnosis.—*Wedoquella* es próximo a *Phiale* C. L. Koch, 1846 y puede ser reconocido principalmente por los caracteres de la genitalia masculina. Se diferencia de *Phiale* por presentar dos apófisis en la tibia del palpo. De las especies de *Phiale* del grupo *gratiosa* se distingue por tener el émbolo recto y mucho más corto y el fémur más ancho. De las especies de *Phiale* del grupo *mimica* se diferencia por tener el émbolo más corto y ancho, y el fémur más largo que el cymbium.

Descripción.—Largo total 4.8-10.6. Ancho del prosoma 70-79% del largo. Alto del prosoma 41-51% del largo. Largo del área ocular 39-48% del largo del prosoma. Lados paralelos o levemente convexos en la región torácica. Área ocular más ancha que larga; en las hembras apenas más ancha atrás; en los machos levemente más ancha atrás, paralela (*W. macrothecata* sp. n.), o levemente más ancha adelante (*W. punctata* y *W. denticulata* sp. n.). OMP próximos a OLA. Clípeo angosto, apenas un tercio o un cuarto del diámetro de OMA. Estría torácica poco detrás de OLP. Esternón truncado adelante apenas más angosto que la base del labio. Láminas maxilares con el ángulo externo saliente, sin apófisis ni mucrones. Quelíceros paralelos, verticales; promargen con dos dientes (excepto *W. macrothecata* macho adulto); retromargen con un diente. Largo relativo de las patas, machos 1432, hembras 4312. Tibia más patella 4 siempre más largas que tibia más patella

3. Muchas y fuertes espinas; los machos a menudo con dorsales en tibias 3 y 4. Palpo con fémur muy ancho (50-60% del largo) algo curvado, con el dorso cubierto por pelos blancos. Tibia con dos apófisis retrolaterales: una inferior, levemente flexuosa y otra superior, piramidal, a veces con denticulos en la arista externa (*W. denticulata*). Bulbo oval, base bilobada. Embolo de inserción prolateral apical, recto, corto, dirigido hacia el ápice del cymbium. Epigino con bolsillo impar de anclaje en el borde posterior y orificios de entrada a los conductos en fosas ampliamente separadas. Prosoma pardo oscuro o negro, con bandas laterales y banda media de pelos blancos o amarillos; opistosoma con dos bandas dorsales pardas o negras, separadas por una banda longitudinal amarilla. Algunas hembras con el dorso totalmente cubierto por pelos rojos.

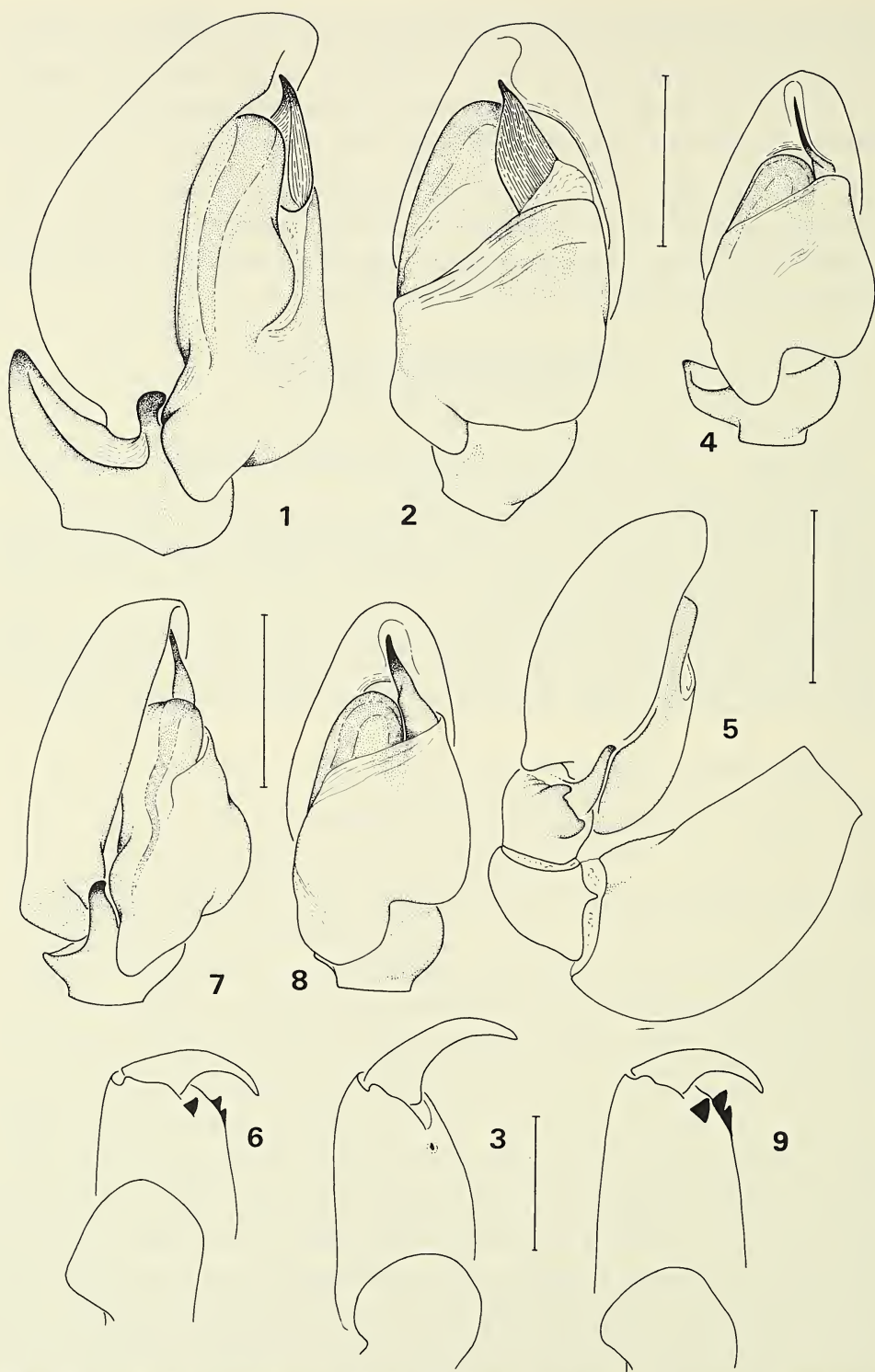
Wedoquella denticulata, nueva especie
(Figs. 4-6, 10, 11, 16, 17)

Etimología.—El nombre proviene del latín *denticulatus*, dentellado, y se refiere a los denticulos de la apófisis tibial superior del palpo.

Diagnosis.—Se diferencia de las otras dos especies del género por tener la apófisis tibial superior de tamaño intermedio, con el borde exterior dentellado; el émbolo más delgado que en esas especies; fosas del epigino circulares, no elípticas como las de *W. macrothecata* y sin las carenas de *W. punctata*.

Descripción.—Largo total, machos 5.4-7.5; hembras 7.5-8. Ancho del prosoma, machos 73-79% del largo; hembras 72-77%. Alto del prosoma, machos 45-51% del largo; hembras 44-47%. Largo del área ocular, machos 42.5-47.6% del largo del prosoma; hembras 39-43.7%.

Holotipo macho.—Largo total 6.00. Prosoma, largo 2.60, ancho 1.97, alto 1.20. Clípeo, alto 0.13. Estría torácica 0.10 más atrás de OLP. Área ocular largo 1.15; ancho de hilera anterior 1.63; de hilera posterior 1.62. Distancia OLA-OMP 0.30; OMP-OLP 0.33. Diámetro OMA 0.57. Quelíceros: promargen con dos dientes; retromargen con uno. Quetotaxia: Fémures I d 1-1-1, p 2, r 2; II d 1-1-1, p 2, r 1-2; III, IV d 1-1-1, p 1-2, r 1-2. Patellas I, II p 1; III, IV p 1, r 1. Tibias I v 2-2-2, p 1-1, r 1-1; II v 2-2-2, p 1-1-1, r 1-1; III, IV d 1, v 2-2, p 1-1-1-1, r 1-1-1-1. Metatarsos I, II v 2-2, p 1, r 1; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. Palpos: cymbium con una prolongación dorsal basal cónica, roma. Apófisis tibial superior con denticulos irregulares en borde externo. Apófisis tibial inferior larga, delgada, flexuosa. Lóbulo retrolateral del bulbo bien desarrollado. Embolo más ancho en la base que en el ápice, con leve torsión (Figs. 4, 5, 10, 11). Color: prosoma pardo oscuro con la región cefálica negra. En la línea media, una ancha banda de pelos amarillos desde cerca del margen anterior hasta la mitad del declive torácico, ensanchándose sobre la estría. Bandas marginales amarillas con pelos amarillos, que hacia adelante ocupan todo el espacio bajo los OLA. Clípeo desnudo, salvo escasos pelitos pardos. En margen anterior, pelos blancos entre OMA y por fuera de OLA. El resto del prosoma cubierto por pelos negros. Opistosoma con dos anchas bandas pardas cubiertas por pelos negros, separadas entre si y limitadas exteriormente por bandas amarillas con pelos amarillos. Las bandas pardas no se tocan ni en la base ni en el ápice. Vientre pardusco. Quelíceros pardo rojizo oscuro. Pata I con fémur amarillo, con cara retrolateral negra con pelos negros y el ápice oscurecido; patella y tibia pardo oscuro, ésta con un anillo mediano de pelos blancos; metatarso y tarso pardo claro. Fémures II a IV blanco-amarillento, oscurecidos en el ápice hacia retrolateral; patellas, tibias y metatarsos pardos con abundantes pelos blancos en prolateral; tarsos amarillentos.



Figs. 1-9.—*W. macrothecata*, holotipo macho: 1, palpo, retroventral; 2, ventral; 3, quelícero. *W. denticulata*, holotipo macho: 4, palpo, ventral; 5, retrolateral; 6, quelícero. *W. punctata*, macho: 7, palpo, retroventral; 8, ventral; 9, quelícero. Escala 0.5 mm.

Paratipo hembra N° 7534 MACN.—Largo total 8.78. Prosoma, largo 3.60, ancho 2.93, alto 1.67. Clípeo alto 0.13. Estría torácica 0.10 más atrás de OLP. Area ocular: largo 1.53; ancho de hilera anterior 2.13; de hilera posterior 2.20. Distancia OLA-OMP 0.33; OMP-OLP 0.50. Diámetro OMA 0.70. Quelíceros: promargen con dos dientes; retro-margen con uno. Quetotaxia: Fémures I d 1-1-1, p 2; II d 1-1-1, p 2, r 1-2; III d 1-1-1, p 1-2, r 1; IV d 1-1-1, p 1, r 1. Patellas I 0; II p 1; III, IV p 1, r 1. Tibias I v 2-2-2, p 1; II v 1-2-2, p 1-1; III, IV v 1-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. Epigino: fosas circulares, ampliamente distanciadas, sin carenas. Espermatecas circulares (Figs. 16 y 17). Color: esencialmente como el macho, con estas excepciones: los pelos de las bandas claras son blanquecinos en lugar de amarillos. En los costados del opistosoma, las bandas laterales tienen dos ensanchamientos apicales. Vientre con banda media negruzca. Patas con fémures amarillos, negruzcos en el tercio apical; patellas y tibias I pardas, con las caras laterales más oscuras; metatarsos y tarsos amarillos. Las otras patas como I, pero más claras. Palpos blanquecinos con pelos blancos.

Variaciones.—En otros ejemplares, las siguientes diferencias en la quetotaxia: machos, fémur I r 1. Patella II r 1. Tibia II r 1-1-1; III, IV p 1-1-1, r 1-1-1. Hembras, tibia I p 1-1. En algunas hembras, los pelos de la región cefálica son rojizos y en el opistosoma la totalidad de la superficie está cubierta por pelos rojos, aunque debajo se transparentan las bandas pardas del tegumento. En los costados, los pelos rojos se mezclan con pelos amarillos. El vientre es amarillo, con una o dos bandas medias negruzcas.

Observaciones.—Ejemplares hembras ovíplenos de esta especie desovaron en el laboratorio y las crías llegaron a adultas. El ejemplar hembra paratipo N° 7534 MACN es la madre del holotipo macho.

Localidad típica.—R. Argentina: provincia de Misiones; Parque Nacional Iguazú.

Distribución geográfica.—R. Argentina: Misiones; Parque Nacional Iguazú; General Belgrano; Puerto Esperanza.

Material estudiado.—R. ARGENTINA: *Misiones*; Parque Nacional Iguazú, noviembre 1981 (M. E. Galiano), 1 macho holotipo N° 7533 (MACN), 1 hembra partipo N° 7534 (MACN), 1 hembra paratipo N° 7535 (MACN), 2 machos paratipos (MEG), octubre 1978 (M. E. Galiano), 2 machos, 3 hembras paratipos N° 7536 (MACN), octubre 1977 (M. E. Galiano), 2 machos, 4 hembras paratipos N° 7537 (MACN), 2 machos, 2 hembras paratipos (MEG), octubre 1979 (M. E. Galiano), 1 macho paratipo N° 800 (MEG), 3 machos, 1 hembra paratipos (MCZ); General Belgrano, diciembre 1972 (M. E. Galiano), 1 macho, 1 hembra paratipos N° 7538 (MACN), 1 hembra paratipo N° 578 (MEG); Puerto Esperanza, setiembre 1978 (G. Williner), 7 machos, 1 hembra N° 7539 (MACN).

Wedoquella macrothecata, nueva especie

(Figs. 1-3, 12, 13, 20, 21)

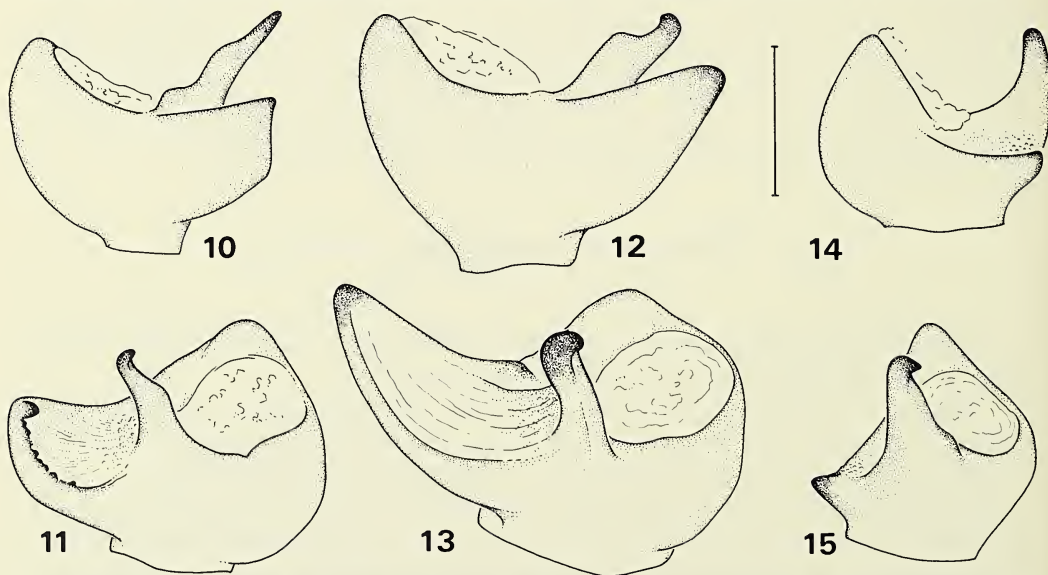
Etimología.—El nombre proviene del griego *macros*, amplio, grande y del latín *theca*, estuche, caja. Se refiere al gran tamaño de las espermatecas.

Diagnosis.—Se diferencia de las otras dos especies del género por tener el émbolo muy ancho y aplanado, la apófisis tibial superior muy desarrollada, las espermatecas grandes y los orificios de entrada a los conductos en el fondo de fosas elípticas oblicuas.

Descripción.—Largo total, machos 7-7.7; hembras 7-10.6. Ancho del prosoma, machos 71-79% del largo; hembras 70-74.5%. Alto del prosoma, machos 43-50% del largo; hembras 41-45.5%. Largo del área ocular, machos 43-48% del largo del prosoma; hembras 41.5-43%.

Holotipo macho.—Largo total 7.05. Prosoma, largo 3.00, ancho 2.13, alto 1.33. Clípeo, alto 0.13. Estría torácica 0.13 más atrás de OLP. Area ocular: largo 1.30; ancho de las hileras anterior y posterior 1.83. Distancia OLA-OMP 0.33; OMP-OLP 0.36. Diámetro OMA 0.63. Quelíceros con el surco ungual algo oblicuo; promargen sin dientes; retromargen con un dentículo pequeño (Fig. 3). Quetotaxia: Fémures I d 1-1-1, p 2; II d 1-1-1, p 2, r 1; III d 1-1-1, p 1-2, r 2; IV d 1-1-1, p 1, r 1. Patellas I, II p 1; III, IV p 1, r 1. Tibias I v 2-2-2, p 1-1; II v 1-2-2, p 1-1; III, IV v 1-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. Palpos: apófisis tibial superior muy desarrollada; apófisis inferior corta, doblada en el ápice. Lóbulo externo del bulbo, reducido. Embolo muy ancho, negro, aplanado, estriado longitudinalmente (Figs. 1, 2, 12, 13). Color: prosoma pardo con la región cefálica negruzca. De cada lado una ancha banda marginal amarilla o pardo claro con pelos amarillos, que se prolonga hacia adelante y ocupa todo el espacio bajo OLA. Clípeo con escasos pelos amarillos. En el margen anterior del prosoma, entre OMA y por delante de OLP, algunos pelos blancos. Por fuera de OMA y OLA, pelos rojos. En la mitad anterior de la región torácica, sobre la estría, pelos blancos. El resto del prosoma, con pelos negros. Quelíceros pardo rojizo con largos pelos amarillos, escasos, en la cara anterior. Opistosoma con dos anchas bandas dorsales longitudinales, cubiertas por pelos negros. Entre ambas y limitándolas externamente, bandas amarillas con pelos amarillos. Vientre pardo, hileras negras. Patas I pardo rojizo oscuro, con cara inferior de fémures amarilla. Las otras patas amarillas, extremo de fémures, base y ápice de tibias y metatarsos, oscurecidos. Palpo, fémur amarillo cubierto dorsalmente por largos pelos blancos; patella y tibia pardo claro, cymbium pardo oscuro.

Paratipo hembra Nº 7541 MACN.—Largo total 7.71. Prosoma, largo 3.40, ancho 2.53, alto 1.47. Clípeo, alto 0.13. Estría torácica 0.07 más atrás de OLP. Area ocular: largo 1.43; ancho de hilera anterior 2.02; de hilera posterior 2.16. Distancia OLA-OMP 0.37; OMP-OLP 0.47. Diámetro OMA 0.70. Quelíceros: cara anterior bastante convexa. Promargen con dos dientes; retromargen con uno. Quetotaxia: Fémures I, II d 1-1-1, p 2; III d 1-1-1, p 1-2, r 1. Patellas I, II p 1; III, IV p 1, r 1. Tibias I v 2-2-2, p 1-1; II v 1-1-2,



Figs. 10-15.—Tibias del palpo. *W. denticulata*: 10, dorsal; 11, retroventral. *W. macrothecata*: 12, dorsal; 13, retroventral. *W. punctata*: 14, dorsal; 15, retroventral. Escala 0.25 mm.

p 1-1; III, IV v 1-2, p 1-1-1, r 1-1-1. Metatarsos I, II v 2-2; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. Epigino: placa de gran tamaño, con dos fosas elípticas, oblicuas, muy distanciadas entre si en la mitad anterior. Espermatecas ovoideas, muy grandes (Figs. 20 y 21). Color: prosoma pardo anaranjado con la región cefálica algo más oscura, totalmente cubierta por finos pelitos blancos, no muy densos, hasta el comienzo del declive. No hay bandas marginales. El espacio bajo OLA ocupado por pelos blancos amarillentos, que forman una barba poco densa en el clípeo. Opistosoma esencialmente como en el macho, excepto que el vientre lleva una banda media amarilla. Esternón y piezas bucales anaranjados. Patas amarillas, algo anaranjadas en tibias y metatarsos. Palpos amarillos con pelos blancos.

Variaciones.—En otros ejemplares, las siguientes diferencias en la quetotaxia: machos, fémur II p 1, r 1; IV p 2. Patella I p 0. Hembras, fémur II r 1. Tibia II v 1-2-2. En algunos machos, hay escasos pelos rojos mezclados con los negros que cubren las bandas del dorso. En ciertas hembras, los pelos de estas bandas son pardo rojizo.

Observaciones.—El ejemplar hembra paratipo N^o 7541 MACN que aquí se describe construyó una ooteca en el laboratorio, de donde salieron crías que alcanzaron el estado adulto. Uno de esos ejemplares se describe como holotipo macho de la especie. Los especímenes juveniles de ambos sexos tienen quelíceros con dos dientes en promargen y uno en retromargen, bien desarrollados. Con la realización de la última muda se produce en el macho la modificación en la dentición que lleva a la pérdida de los dientes promarginales y a la reducción del retromarginal. En un ejemplar se vieron dos dentículos en el lugar de los dientes del promargen.

Localidad típica.—R. Argentina: provincia de Misiones; Parque Nacional Iguazú.

Distribución geográfica.—R. Argentina: Misiones; Parque Nacional Iguazú; San Javier; Tobuna; Puerto Libertad; Puerto Esperanza; Santa María.

Material estudiado.—R. ARGENTINA: *Misiones*; Parque Nacional Iguazú, octubre 1979 (M. E. Galiano), 1 macho holotipo N^o 7540 (MACN), 1 hembra paratipo N^o 7541 (MACN), 1 macho, 3 hembras paratipos (MEG), octubre 1978 (M. E. Galiano), 1 macho, 2 hembras (MEG), noviembre 1970 (M. E. Galiano), 1 macho, 2 hembras paratipos (MCZ); Puerto Esperanza, agosto 1978 (G. Williner), 2 machos, 2 hembras paratipos N^o 7542 (MACN); Puerto Libertad, octubre 1953 (Schiapelli, Galiano), 1 hembra N^o 7544 (MACN); Tobuna, octubre 1953 (W. Partridge), 1 macho N^o 7545 (MACN); Santa María, setiembre 1956 (M. Viana), 2 hembras N^o 7546 (MACN); *Corrientes*; Ituzaingó, octubre 1981 (M. Fritz), 1 macho N^o 7547 (MACN).

Wedoquella punctata (Tullgren, 1905) nueva combinación

(Figs. 7-9, 14, 15, 18, 19)

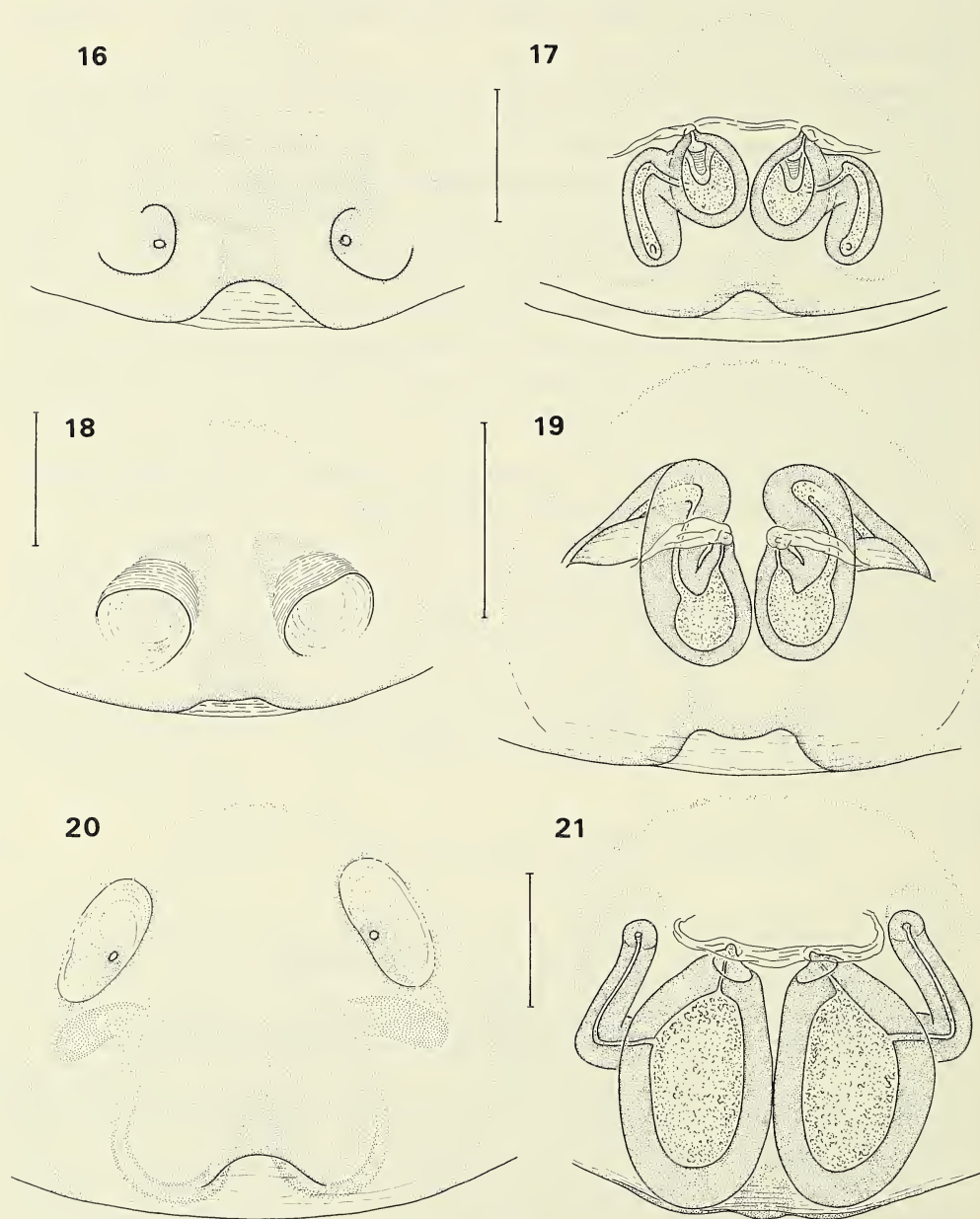
Euophrys (?) *punctata* Tullgren 1905:74, pl. 10, f. 39 (hembra holotipo de Bolivia: Dto. Tarija; Tatarenda, Chaco Cord. Sv. Exp., en NRS, examinado); Petrunkevitch 1911:648 (*Evophrys*); Roewer 1954:1181; Bonnet 1956:1887 (*Evophrys*).

Pensacola variegata Mello-Leitão 1939:89, f. 80 (hembra holotipo de Paraguay, Ternetz col., N^o 1212a en MHN, examinado); Roewer 1954:1145; Bonnet 1958:3840. NUEVA SINONIMIA.

Diagnosis.—Se diferencia de *W. denticulata* por la gran reducción de la apófisis tibial superior, el mayor tamaño del proceso dorsal basal del cymbium y el gran desarrollo de las carenas en el borde superior de las fosas del epigino.

Descripción.—Largo total, machos 4.8-8.2; hembras 6.6-10.10. Ancho del prosoma 71-78.5% del largo; hembras 72-77%. Alto del prosoma, machos 44-47% del largo; hembras 42-46.5%. Largo del área ocular, machos 39-45% del largo del prosoma; hembras 41.5-42%.

Holotipo hembra.—Prosoma largo 2.80, ancho 2.10, alto 1.33. Clípeo alto 0.10. Área ocular: largo 1.23; ancho de hilera anterior 1.70; de hilera posterior 1.77. Distancia OLA-OMP 0.30; OMP-OLP 0.33. Diámetro OMA 0.57. Quelíceros: promargen con dos dientes; retromargen con uno. Quetotaxia: Patella I, II 0; III, IV p 1, r 1. Tibia I v 2-2-2; II v 1-2-2; III, IV v 1-2, p 1-1-1, r 1-1-1. Metatarso I, II v 2-2; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. Epigino: fosas profundas, con ancha carena en el borde superior (Figs. 18 y 19). Quetotaxia y color en otros ejemplares hembras.—Fémures I d 1-1-1, p



Figs. 16-21.—Epiginos y espermatecas. *W. denticulata*: 16 y 17. *W. punctata*: 18 y 19. *W. macrothecata*: 20 y 21. Escala 0.25 mm.

2; II d 1-1-1, p 2, r 1-1; III d 1-1-1, p 1-2, r 1; IV d 1-1-1, p 1, r 1. Tibia I p 1; II p 1-1; III, IV v 1-2. Prosoma pardo oscuro con la región cefálica negruzca. De cada lado una anchísima banda amarilla con pelos blancos, que adelante ocupa todo el espacio bajo los OLA. Clípeo desnudo o con escasos pelitos blancos. En la línea media dorsal una banda de pelos blancos desde el margen anterior hasta la mitad del declive torácico. Algunos pelos blancos alrededor de OLP y rojos por fuera de OLA. Resto del prosoma cubierto por pelos negros, con algunos blancos y rojos mezclados. Opistosoma pardo, con una banda media en la mitad basal, angosta, amarilla, seguida de cuatro bandas transversas en forma de V invertida. En cada costado, una banda basal amarilla seguida de dos grandes manchas. Toda la superficie de dorso y costados cubierta por pelos negros, amarillos, blancos y rojos mezclados, con predominio de negros en las partes pardas y amarillos en las partes amarillas. Vientre amarillo con banda media negruzca. Quelíceros rojizos, piezas bucales y esternón, pardos. Pata I amarilla, con mitad apical de fémur, patella y tibia, pardos. Las otras patas amarillas; III y IV con ápice de fémures y tibias negruzcos. Palpos amarillos con pelos blancos. En las hembras depiladas o con el opistosoma muy distendido por los huevos, las manchas claras se hacen mucho más evidentes. Algunas hembras tienen prosoma (con excepción de las bandas laterales) y opistosoma, cubiertos dorsalmente por pelos rojos, bajo los cuales puede advertirse el diseño básico descripto.

Macho N° 7554 MACN.—Largo total 6.26. Prosoma largo 2.90, ancho 2.17, alto 1.40. Clípeo alto 0.13. Estría torácica 0.10 más atrás de OLP. Area ocular: largo 1.22; ancho de hilera anterior 1.73; de hilera posterior 1.72. Distancia OLA-OMP 0.30; OMP-OLP 0.36. Diámetro OMA 0.60. Quelíceros: promargen con dos dientes; retromargen con uno. Quetotaxia: Fémures I d 1-1-1, p 2, r 1; II d 1-1-1, p 2, r 1-2; III d 1-1-1, p 1-2, r 1-2; IV d 1-1-1, p 1-2, r 2. Patellas I-IV p 1, r 1. Tibias I v 2-2-2, p 1-1, r 1-1; II v 1-2-2, p 1-1, r 1-1; III, IV d 1, v 1-2, p 1-1-1-1, r 1-1-1-1. Metatarsos I v 2-2; II v 2-2, p 1; III v 2-2, p 1-2, r 1-1-2; IV v 2-2, p 1-1-2, r 1-1-2. Palpos: cymbium con un proceso basal dorsal muy desarrollado, aplanado dorso-ventralmente. Apófisis tibial superior reducida; apófisis inferior cónica, levemente curvada en el ápice (Figs. 7, 8, 14, 15). Color: prosoma con pelos negros, bandas laterales y media con pelos amarillos. Opistosoma con el mismo diseño básico que el de las hembras. Los pelos que cubren la superficie forman un diseño independiente del dibujo del tegumento, ya que hay dos anchas bandas longitudinales de pelos negros, separadas por una angosta banda de pelos amarillos y externamente limitadas por bandas amarillas. El diseño de manchas del tegumento solo es visible en ejemplares depilados o en alcohol. Quelíceros pardo negruzco, piezas bucales y esternón, pardos. Patas I pardo oscuro, metatarsos y tarsos pardo claro. Otras patas amarillas, con ápice de fémures y tibias, negruzcos. Palpo con fémur pardo claro, dorso con pelos blancos; el resto pardo oscuro.

Localidad típica.—Bolivia: Departamento Tarija; Tatarenda.

Distribución geográfica.—Bolivia: Dto. Tarija. Paraguay: Caá-Guazú. R. Argentina: Misiones: Salta: Formosa.

Material estudiado.—R. ARGENTINA: *Salta*: San Pedro, noviembre 1951 (M. Birabén), 1 macho N° 7548 (MACN); *Misiones*: Puerto Libertad, noviembre 1954 (Schiapelli, Galiano), 1 macho N° 7549 (MACN); San Antonio, noviembre 1961 (A. Martínez), 3 machos, 5 hembras N° 7552 (MACN), noviembre 1970 (M. E. Galiano), 1 macho N° 7557 (MACN); San Javier, diciembre 1948 (M. Birabén), 3 machos, 1 hembra N° 7553 (MACN); Parque Nacional Iguazú, diciembre 1972 (M. E. Galiano), 2 hembras N° 7556 (MACN), octubre 1979 (M. E. Galiano), 1 macho N° 7554 (MACN); *Formosa*, diciembre 1954, 1 macho N° 7551 (MACN). PARAGUAY: *Caá-Guazú*: Piscicultura, diciembre 1977 (Martínez, Fritz), 1 hembra N° 7550 (MACN).

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THE PSEUDOSCORPIONS DESCRIBED BY R. V. CHAMBERLIN (PSEUDOSCORPIONIDA, OLPIIDAE AND CHERNETIDAE)

William B. Muchmore

Department of Biology
University of Rochester
Rochester, New York 14627

ABSTRACT

The four species of pseudoscorpions described by R. V. Chamberlin in 1925, but neglected since that time, are redescribed and placed in modern context. They are now *Pachyolpium isolatum*, *Lustrochernes consocius*, *Chelodamus atopus*, and *Chelodamus mexicolens*. The genus *Chelodamus* is redefined and *Chelanops atopus* Banks is newly assigned to it.

INTRODUCTION

In a paper concerning a number of arachnids from Central America, R. V. Chamberlin (1925) described four new species of pseudoscorpions, namely, *Olpium isolatum*, *Chelanops consocius*, *Chelodamus atopus* and *Chelodamus mexicolens*, the latter two belonging to a new genus. However, for some unexplained reason, this paper has been ignored by most subsequent workers, the only exceptions being an acknowledgment by J. C. Chamberlin (1931:242) of the generic name *Chelodamus* and citations of the specific name *Chelodamus mirabilis* in synonymies by Hoff (1946:201) and Muchmore (1974:30). As a result of this neglect, the species involved have not been properly considered in the relevant literature. It is the purpose of the present paper to discuss the importance of these forms in relation to others which have been described since that time.

FAMILY OLPIIDAE CHAMBERLIN

Pachyolpium isolatum (R. V. Chamberlin), new combination
Fig. 1

Olpium isolatum R. V. Chamberlin, 1925:239, no Fig. Holotype female (WM 1949.010001) from Largo Remo Island, Canal Zone, Panama, in MCZ. The specimen has been cleared, dissected, mounted on a microscope slide, and examined.

Pachyolpium adiposum Hoff, 1945:12, Figs. 15, 16. Holotype female from Barro Colorado Island, Canal Zone, Panama, in AMNH, examined. **NEW SYNONYMY.**

Description of female (male unknown).—The holotype of *O. isolatum* is very similar to the female from Barro Colorado Island which Hoff described as *P. adiposum*. Because Chamberlin's and Hoff's descriptions taken together are so detailed, only the major features of interest will be mentioned here.

Carapace with an indistinct transverse furrow; with about 30 setae. Tergal chaetotaxy 4:6:9:9:12?:12:11:12:10?:2; sternal chaetotaxy 6:(0)4(0):(0)6(0):11:10:----. Cribiform plates not visible.

Chelicera 2/5 as long as carapace; hand with five long, acuminate setae; flagellum of three denticulate setae; galea with three slender rami (distorted by prior drying).

Palp with femur 2.45, tibia 2.1, and chela 2.65 times as long as broad; hand 1.5 times as long as deep; movable finger 0.97 as long as hand. Femur with a conspicuous tactile seta on dorsum about 1/3 distance from proximal end. Trichobothria as shown in Fig. 1; *ist* near base of fixed finger at level of *isb*. Venom apparatus well developed in both fingers; in fixed finger nodus ramosus of venom duct just proximad of trichobothrium *et*; in movable finger nodus ramosus about midway between *t* and finger tip. Fixed finger with 45 and movable finger with 44 marginal teeth; on both fingers teeth are flattened and acuspid proximally.

Legs moderately robust; leg IV with entire femur 2.75 times as long as deep. Leg I with basifemur 1.5 times as long as telofemur. Metatarsus IV with long tactile seta 1/6 distance from proximal end.

Measurements (mm) of mounted holotype.—Body length 3.18. Carapace length 0.70. Chelicera length 0.30. Palpal femur 0.59 by 0.24; tibia 0.60 by 0.285; chela (without pedicel) 1.06 by 0.40; hand 0.57 by 0.385; pedicel 0.10 long; movable finger 0.55 long. Leg I: basifemur 0.305 by 0.11; telofemur 0.20 by 0.125. Leg IV: entire femur 0.66 by 0.24; tibia 0.47 by 0.135; metatarsus 0.24 by 0.08; telotarsus 0.175 by 0.075.

Remarks.—The measurements given here are somewhat greater than those recorded by Chamberlin (1925:239). The difference is probably due to the fact that Chamberlin

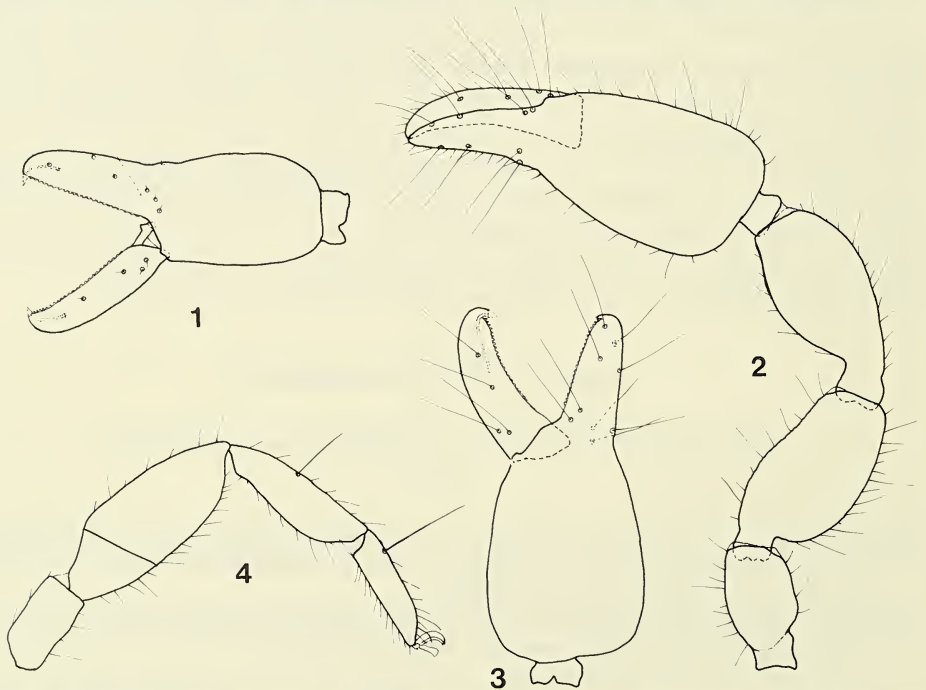


Fig. 1.—*Pachyolpium isolatum* (R. V. Chamberlin), holotype female: lateral view of left palpal chela (slightly tilted toward top).

Figs. 2-4.—*Lustrochernes consocius* (R. V. Chamberlin), holotype female: 2, dorsal view of right palp; 3, lateral view of left chela; 4, lateral view of leg IV.

measured the specimen entire, in alcohol, whereas I measured the dissected parts mounted in favorable positions on a slide.

The holotype female of *P. adiposum* Hoff (from Barro Colorado Island, Panama Canal Zone) has been examined and compared with the holotype female of *O. isolatum*. There is no doubt about their being conspecific. Though the characteristics of the genus *Pachyolpium* Beier are still not clearly defined (cf. Mahnert and Schuster 1981), this species belongs to the genus as diagnosed by Hoff (1964). I consider that the important parts of this diagnosis are the position of trichobothrium *ist* near the base of the fixed finger and the presence of 10-12 setae on the middle tergites of the abdomen. Also diagnostic, I consider, though not recognized previously, is the length of the venom ducts in the chelal fingers, with the nodus ramosus in the fixed finger occurring at or just proximad of trichobothrium *et*.

FAMILY CHERNETIDAE MENGE

Lustrochernes consocius (R. V. Chamberlin), new combination Figs. 2-4

Chelanops consocius R. V. Chamberlin, 1925:238, no Fig. Holotype female (*not* a male as stated by Chamberlin) (WM 1900.01001) from Barro Colorado Island, Canal Zone, Panama, in MCZ. The specimen has been cleared, dissected, mounted on a microscope slide, and examined.

Other material examined.—One male, also from Barro Colorado Island, 11-17 December 1974, K. W. Cooper, in FSCA.

Description.—The original description by Chamberlin is generally accurate but quite brief; therefore, a full account is given here of the holotype female, together with some comments about the male, which is generally very similar. Palps reddish brown, other parts lighter. Dorsal setae acuminate or with few small subterminal spinules, ventral setae acuminate. Carapace about as long as wide; surface smooth; eye spots very faint; anterior transverse furrow distinct, posterior one very faint; with about 70 setae, six at anterior and 16 at posterior margin. Abdomen elongate; tergites and sternites divided; surfaces smooth; pleural membranes longitudinally striate. Tergal chaetotaxy about 22:20:20:24:26:28:28:30:28:26:14:2; sternal chaetotaxy about 18:(3)12(3):(1)8(1):23:32:36:32:30:28:12:2; anterior genital operculum with central cluster of 12 small setae and few posterolaterally; anterior operculum of male with five long central setae surrounded by 17 smaller ones; posterior operculum with two pairs of small setae just inside anterior margin and 12 on face. Spermathecae of female in poor position to reveal details, but apparently similar to those of other species of *Lustrochernes*. Internal genitalia of male without obvious distinguishing characters.

Chelicera about 2/5 as long as carapace; hand with five setae; flagellum of three setae; (galea broken); serrula exterior of 23 blades.

Palp heavy (Fig. 2); femur 2.15, tibia 2.2, and chela 2.5 times as long as wide; hand 1.35 times as long as deep; movable finger 0.78 as long as hand; palp of male more robust in all segments. Surfaces smooth except fine granules on flexor sides of femur, tibia, and hand at base of fingers; trochanter with a prominent dorsal protuberance. Trichobothria as shown in Fig. 3, *et* lying distad of middle of fixed finger and *it* closer to finger tip than distance between *ist* and *isb*. Venom apparatus well developed only in movable finger, nodus ramosus about midway between trichobothria *t* and *st*. Fixed finger with 35 and

movable finger with 34 contiguous, cusped teeth; each finger with 3-4 internal and 10-11 external accessory teeth.

Legs moderately slender; leg IV (Fig. 4) with entire femur 2.7, tibia 3.7, and tarsus 4.15 times as long as deep. Tibia IV with a conspicuous tactile seta just proximad of middle and tarsus IV with a larger tactile seta about 1/5 distance from proximal end.

Measurements (mm).—Figures given first for the holotype female, followed in parentheses by those for the topotype male. Body length 4.1(3.2). Carapace length 1.085(0.97). Chelicera length 0.40(0.385). Palpal femur 0.96(0.89) by 0.445(0.44); tibia 0.96(0.96) by 0.435(0.47); chela (without pedicel) 1.61(1.52) by 0.645(0.63); hand (without pedicel) 0.96(0.85) by 0.70(0.69); pedicel 0.12(0.11) long; movable finger 0.745(0.75) long. Leg IV: entire femur 0.94(0.93) by 0.35(0.31); tibia 0.74(0.72) by 0.20(0.18); tarsus 0.56(0.55) by 0.135(0.13).

Remarks.—The present species is placed in *Lustrochernes* Beier following the considerations mentioned by Muchmore (1976). *Lustrochernes* may be separated from *Americhernes* Muchmore by the placement of trichobothria on the fixed chelal finger; and it is distinguished from both *Cordyllochernes* Beier and *Mesochernes* Beier in having less slender legs, e.g., tarsus IV being less than 5 times as long as wide (Beier 1932:82).

About a dozen species of *Lustrochernes* have been reported from Central America. The definitions of most of these are unsatisfactory by virtue of being very brief or based on only one or two specimens. As there is typically a considerable amount of variation in size and proportions and significant sexual dimorphism in some species of *Lustrochernes* (Hoff 1956; Mahnert 1979; personal observation), it is impossible at this time to determine whether any of the other species are the same as *L. consocius*. Sorting out the species in this genus and in the closely related *Cordyllochernes* and *Mesochernes* must await extensive detailed reexamination and comparison of the many forms involved.

Genus *Chelodamus* R. V. Chamberlin

Chelodamus R. V. Chamberlin, 1925:236. Type species, *Chelodamus atopus* R. V. Chamberlin 1925:237.

Pseudozaona Beier, 1932:182, 1933:542; Hoff 1947:539, 1949:471; Hoff and Bolsterli 1956:170. Type species, *Pseudozaona communis* Beier 1932:182. NEW SYNONYMY.

Diagnosis (revised).—A genus of the family Chernetidae. Of moderately large size; generally heavily sclerotized, therefore, dark in color, with palps and carapace reddish to dark brown; surfaces distinctly granulate or scaly; dorsal setae clavodentate, ventral setae acuminate. Carapace with two transverse furrows; two weak eyespots; with up to 150 setae. Abdominal tergites and sternites divided (contrary to the statement of Chamberlin); pleural membranes strongly papillose; middle tergites and sternites with 16-22 setae, sometimes irregularly placed; 11th sternite may have two or four acuminate, tactile setae, 11th tergite may have two such setae. Cheliceral hand with five setae, *sb* terminally denticulate, the others acuminate; flagellum of four setae, denticulate on one margin (*not* three setae, as stated by Chamberlin); galea with 5-6 small rami, slightly less well developed in male. Palp long and slender, "approaching the chelifer type," as Chamberlin notes (1925:236), but less so in male than in female; tibia of male with distinct medial bulge proximad of middle; chelal fingers of male distinctly curved at middle (bowed); on movable chelal finger trichobothrium *st* closer to *t* than to *sb*; on fixed finger *ist* distad of *est*; venom apparatus well developed in movable finger, apparently absent in fixed finger; both fingers well provided with marginal and accessory teeth. Legs rather slender; tarsus

of leg IV without an acuminate tactile seta, but with a conspicuous long, denticulate seta distad of middle. Anterior genital operculum of male with 4-5 long setae surrounded by numerous smaller ones; anterior operculum of female with a group of 10-15 small setae at the center and an equal number scattered posterolaterally; internal genitalia of male of general chernetid type, without obvious distinguishing features; spermathecae of female are two long, thin tubules with ends expanded very little or not at all.

Contrary to the statement of Chamberlin, members of the genus *Chelodamus* have four setae in the cheliceral flagellum. *Chelodamus* is most similar to *Hesperocheernes* Chamberlin (Muchmore 1974), from which it can be distinguished by the following characters: 1) male with palpal tibia having a distinct bulge proximad of the middle and chelal fingers distinctly bowed; 2) spermathecae of female not terminally expanded into an ovoid or spheroid bulb; 3) seta *b* on cheliceral hand acuminate rather than denticulate; 4) appendages, most noticeably the palps, long and slender, rather than short and stout. The last comparison fails in some cave-adapted species of *Hesperocheernes*, such as *H. mirabilis* (Banks) and *H. occidentalis* (Hoff and Bolsterli), where the appendages are attenuated apparently as an accommodation to life in caves. *Chelodamus*, on the other hand, has the appendages elongated to adapt it to living between the leaves of bromeliads, as in *Macrocheernes* Hoff and *Zaona* Chamberlin, for example.

Chelifier mirabilis Banks actually belongs in *Hesperocheernes* (see Muchmore 1974) rather than in *Chelodamus* as suggested by Chamberlin.

Chelodamus atopus R. V. Chamberlin

Figs. 5-8

Chelodamus atopus R. V. Chamberlin, 1925:237, no Fig. Holotype male (WM 1739.01001) from Costa Rica, R. V. Chamberlin Coll. (no other collection data), accompanied by label "Boiled in KOH," in MCZ. One female labelled "*Chelanops atopus* Chamb., Paratype," from Costa Rica, R. V. Chamberlin Coll. (no other collection data), in MCZ. Both specimens have been cleared, dissected, mounted on microscope slides, and examined.

Description.—The original description of the holotype male by Chamberlin is generally accurate but not sufficiently detailed for present purposes. Therefore, a reiteration and clarification of important characters is given here together with some comments about the female. Body and appendages well sclerotized, shades of brown. Surfaces generally granulate or scaly; dorsal setae mostly clavodentate, ventral setae mostly acuminate. Carapace about as long as broad; both transverse furrows distinct; eyespots faint; setae on male difficult to see, perhaps because of the KOH treatment, but female with about 140. Abdomen ovoid; tergites granulate, sternites scaly, pleural membranes heavily papillose. Tergal chaetotaxy 15:13:13:19:20:20:22:21:20:16:8:2; middle tergites with one or two setae on disc in addition to marginal row. Sternal chaetotaxy about 23: (2)5/22(2):(1)15(1):17:16:18:19:18:16:8:2; anterior genital operculum of male with four large central setae surrounded by 19 smaller ones, posterior operculum with 20 small setae on each side at middle of anterior margin; female anterior genital operculum with a group of 15-20 setae at center and about a dozen scattered posterolaterally (Fig. 5). Internal genitalia of male without obvious distinguishing features; spermathecae of female consisting of two long, thin tubules apparently of uniform diameter throughout (Fig. 6).

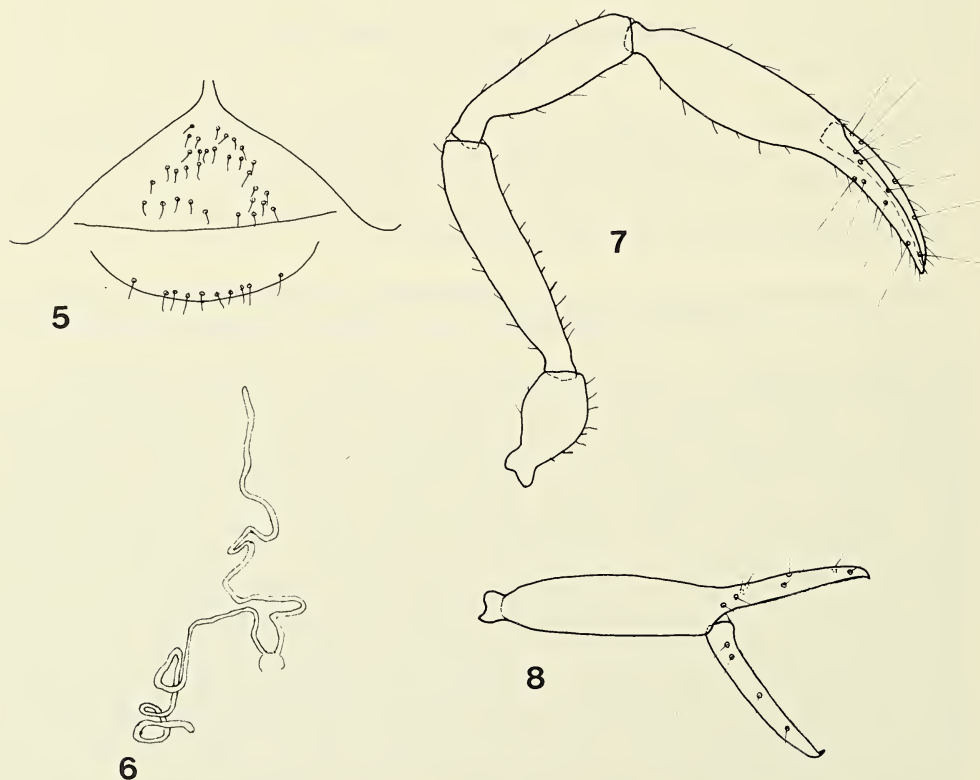
Chelicera 2/7 as long as carapace; hand with five setae, all appearing acuminate; flagellum of four setae (*not* three as reported by Chamberlin), all dentate; galea with five small rami.

Palp (as palps of holotype male have been distorted by the KOH treatment, this description is based mainly on those of the paratype female): long and slender (Fig. 7); femur 5.15, tibia 4.0, and chela 5.25 times as long as wide; hand 3.2 times as long as deep; movable finger 0.85 as long as hand. In spite of the distortion it is clear that tibia of male has distinct bulge proximad of middle on medial side and that movable finger of chela is distinctly curved near middle. Trichobothria on chela as shown in Fig. 8; *ist* distad of *est*, and *st* closer to *t* than to *sb*. Venom apparatus well developed only in movable finger, nodus ramosus closer to trichobothrium *t* than to *st*. Movable finger with about 70 and fixed finger with about 65 contiguous teeth; each finger with 8-12 external and 5-10 internal accessory teeth.

Legs slender; leg IV with entire femur about 4.5, tibia 6.0, and tarsus 5.5 times as long as deep. Tarsus IV without an acuminate tactile seta.

Measurements (mm).—Male and female are quite similar in size; because of the distortion of the holotype male by the KOH treatment, figures are given only for the female paratype. Body length 4.45. Carapace length 1.61. Chelicera length 0.435. Palpal femur 2.11 by 0.41; tibia 1.69 by 0.435; chela (without pedicel) 2.85 by 0.545; hand (without pedicel) 1.59 by 0.495; pedicel 0.20 long; movable finger 1.33 long. Leg IV: entire femur 1.66 by 0.38; tibia 1.10 by 0.18; tarsus 0.725 by 0.125.

Distribution.—Known only from Costa Rica.



Figs. 5-8.—*Chelodamus atopus* R. V. Chamberlin, paratype female: 5, genital opercula; 6, spermathecae; 7, dorsal view of left palp; 8, lateral view of right chela.

Chelodamus mexicolens R. V. Chamberlin

Figs. 9-11

Chelodamus mexicolens R. V. Chamberlin, 1925:238, no Fig. Holotype female (WM 1738.01001) (not a male as stated by Chamberlin) from Guadalajara, Jalisco, Mexico, in MCZ. The specimen has been cleared, dissected, mounted on a microscope slide, and examined.

Pseudozaona communis Beier, 1932:182, Fig. 191; 1933:543, Figs. 13, 14; Muchmore 1974:30. Types (♂ and ♀) from Cameron, Veracruz, Mexico. NEW SYNONYMY.

Other material examined.—One ♀ from Tampico, Veracruz, Mexico, in USNM; 2 ♀ from El Fortin and Potrero, Veracruz, Mexico, in UCD; 1 ♀ from Chichen Itza, Yucatan, Mexico, in MCZ; 3 ♀ from Mt. Pine Ridge, Belize, in MCZ.

Diagnosis.—About same size as *C. atopus* but with less attenuated appendages, e.g., 1/w of palpal femur 4.1-4.3 rather than 5.15.

Description of female (male not available).—Body generally heavily sclerotized; shades of brown; surfaces heavily granulate or scaly; most dorsal setae clavodentate, most ventral setae acuminate. Carapace about as long as broad; both transverse furrows distinct; two small smooth eyespots; about 150 setae. Abdomen ovoid; tergal chaetotaxy of holotype 12:15:11:15:20:20:17:19:17:16:10:2; sternal chaetotaxy 30:(3)11(3):(1)10(1):20:21:22:21:17:14:8:2; others more or less similar. Anterior genital operculum of female with 10-12 setae in group at center and an equal number scattered posterolaterally. Spermathecae are two long, thin tubules with slightly expanded ends (Fig. 9).

Chelicera about 0.3 as long as carapace; hand with five setae, *sb* finely denticulate near tip; flagellum of four setae, all dentate; galea of holotype broken, but in others with 4-6 small rami.

Palp long and slender (Fig. 10) (see Beier 1932:Fig. 191 for male); femur 4.1-4.3, tibia 3.25-3.4, and chela 4.5-4.85 times as long as wide; hand 2.75-3.05 times as long as deep; movable finger 0.9-0.95 as long as hand (Beier, 1932:183, reported ratios for the male of *P. communis* as follows: femur 3.5, tibia 3.0, and chela 4.1). As shown by Beier (1932:Fig. 191), palp of male has tibia with distinct bulge proximad of middle on medial side, and movable finger of chela with distinct curve at middle. Trichobothria on chela as shown in Fig. 11. Movable finger with about 70 and fixed finger with about 65 marginal teeth; each finger with 10-15 internal and external accessory teeth.

Legs slender; leg IV with entire femur 4.1-4.55, tibia 5.5-6.1, and tarsus 5.2 times as long as deep. Tarsus IV without an acuminate tactile seta, but with a conspicuous long, denticulate seta about 2/3 distance from proximal end.

Measurements (mm).—Figures given first for holotype female, followed in parentheses by ranges for the seven available females. Body length 4.8 (3.75-5.1). Carapace 1.54(1.46-1.65). Chelicera length 0.44(0.43-0.465). Palpal femur 1.88(1.68-1.99) by 0.44(0.40-0.465); tibia 1.625(1.46-1.71) by 0.495(0.445-0.54); chela (without pedicel) 2.75(2.55-3.00) by ?(0.54-0.625); hand (without pedicel) 1.47(1.37-1.62) by 0.51(0.47-0.55); pedicel 0.18(0.16-0.19) long; movable finger 1.38(1.31-1.445) long. Leg IV: entire femur 1.53 (1.39-1.58) by 0.335(0.30-0.36); tibia 1.040(0.96-1.10) by 0.17(0.17-0.185); tarsus 0.65(0.63-0.70) by 0.12(0.12-0.13). According to the figures given by Beier (1932:183), the male may be considerably smaller than the female.

Distribution.—Southern Mexico from Jalisco to Yucatan and Belize.

Though not described by R. V. Chamberlin, the following species can also be included in the genus *Chelodamus*.

Chelodamus uniformis (Banks), new combination

Figs. 12-13

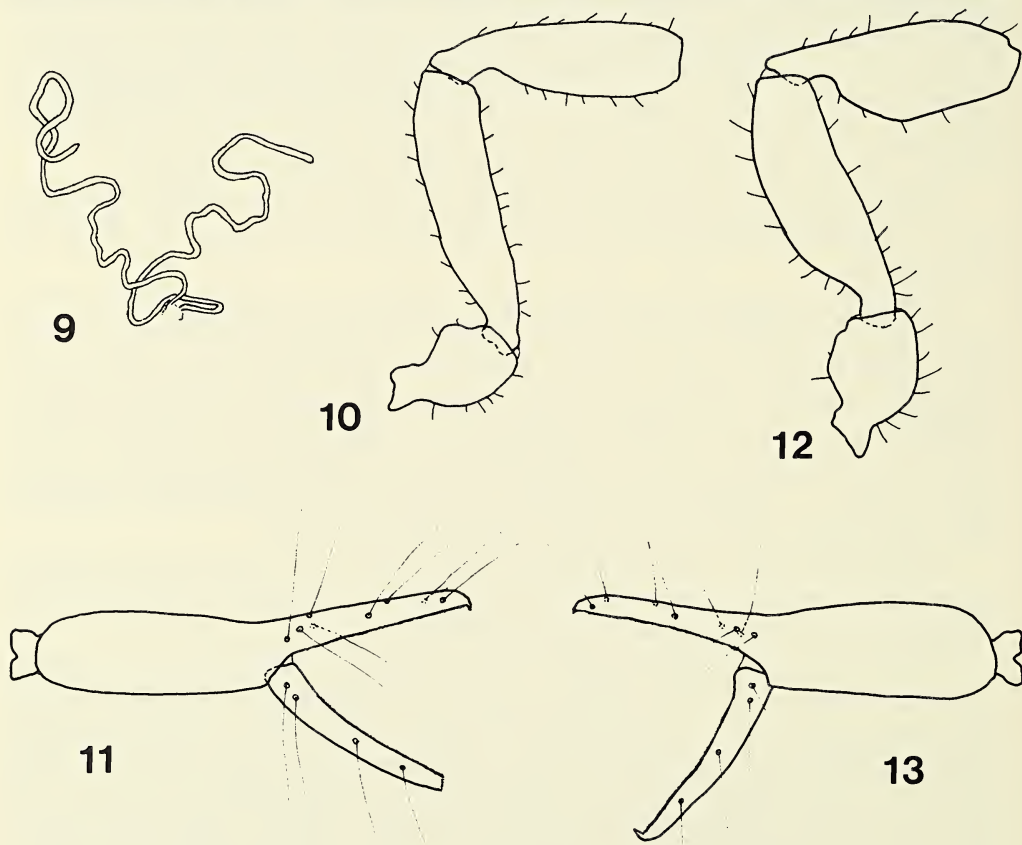
Chelanops uniformis Banks, 1914:683, Figs. 16, 18. Syntypes from La Emilia, Juan Viñas, and Reventazon Valley below Juan Viñas, Costa Rica, in ANSP, MCZ, and USNM: 4 ♂, 4 ♀, 1 tritonymph examined.

Pseudozaona uniformis (Banks); Hoff 1947:540, Figs. 34, 35. One of Banks's syntypes, a female from La Emilia, Costa Rica, designated as lectotype, in MCZ; examined.

Other material examined.—Four ♀ from bromeliad, Coto, Costa Rica, 4 August 1957, E. Dixon, in FSCA.

Diagnosis.—Generally similar to *C. mexicolens* but much smaller (palpal femur less than 1.4 mm in length and chela less than 2.0 mm).

Description.—The description by Hoff based on one female and two males is generally accurate. Some additional observations and measurements will be given here. Male about same size as female but with stouter palps. Carapace with about 100 setae. Tergal



Figs. 9-11.—*Chelodamus mexicolens* R. V. Chamberlin, holotype female: 9, spermathecae; 10, dorsal view of left palpal trochanter, femur and tibia; 11, lateral view of right chela (tip of movable finger broken).

Figs. 12-13.—*Chelodamus uniformis* (Banks), paratype male, 12, dorsal view of left palpal trochanter, femur and tibia; 13, lateral view of left chela.

chaetotaxy of lectotype 9:11:9:16:16:19:16:17:17:18:10:2; sternal chaetotaxy 20:(3)12(3):(1)10(1):16:22:17:18:18:13:9:2; anterior sternal chaetotaxy of male about 22:(3)4/15(3):(1)10(1):---. Anterior genital operculum of female with group of about 10 setae at center and an equal number scattered posterolaterally; spermathecae are long, thin tubules with ends little or not at all expanded. Internal genitalia of male without obvious distinguishing features.

Chelicera about 0.3 as long as carapace; hand with five setae, *sb* terminally denticulate, others acuminate; flagellum of four setae, all denticulate; galea with 5-6 rami.

Palp generally as figured by Banks (1914: Fig. 18) for the male and by Hoff (1947: Fig. 34) for the female. For females, femur 3.5-4.0, tibia 2.8-3.2, and chela 4.0-4.4 times as long as wide; hand 2.35-2.55 times as long as deep; movable finger about 0.95 as long as hand; corresponding ratios for males, femur 3.2-3.5, tibia 2.5-2.65, chela 3.8-4.15, hand 2.1-2.35, and movable finger 0.95. Tibia of male with distinct bulge on medial side proximad of middle (Fig. 12); chelal fingers of male distinctly curved at middle (Fig. 13). Trichobothria as shown in Fig. 13. Movable finger with 60-65 and fixed finger with 55-60 marginal teeth; each finger with 5-10 internal and external accessory teeth.

Leg IV with entire femur 3.6-4.6 and tibia 4.5-5.5 times as long as deep, females more slender than males. Tarsus IV without an acuminate tactile seta but with a prominent, terminally denticulate seta distad of middle.

Measurements.—Ranges for 12 mounted specimens, including lectotype. Body length 2.65-4.05. Carapace length 1.00-1.26. Chelicera 0.31-0.38 long. Palpal femur 1.04-1.39 by 0.305-0.395; tibia 0.93-1.24 by 0.35-0.48; chela (without pedicel) 1.58-2.11 by 0.39-0.51; hand (without pedicel) 0.84-1.14 by 0.38-0.49; pedicel 0.10-0.14 long; movable finger 0.89-1.05 long. Leg IV: entire femur 0.86-1.15 by 0.235-0.28; tibia 0.55-0.79 by 0.125-0.155; tarsus 0.42-0.59 by 0.09-0.11. Males are generally smaller than females.

Distribution.—Known only from Costa Rica.

Remarks.—Also at hand are two males and one female taken from bromeliads at Chamela, Jalisco, Mexico, 31 August 1974, J. R. Napoles. These specimens are intermediate in size and proportions between those known to represent *C. mexicolens* and *C. uniformis*. It is not clear at this time whether they actually represent a separate species or just provide evidence for the synonymy of the two species mentioned.

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Depositories referred to in the text are abbreviated thus: AMNH—American Museum of Natural History, New York, ANSP—Academy of Natural Sciences of Philadelphia, FSCA—Florida State Collection of Arthropods, Gainesville, MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, NMNH—National Museum of Natural History, Washington, UCD—University of California, Davis.

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EVALUATION OF THE LIMB-BEATING SAMPLING METHOD FOR ESTIMATING SPIDER (ARANEAE) POPULATIONS ON APPLE TREES

J. P. McCaffrey¹, M. P. Parrella², and R. L. Horsburgh³

Entomology Department
Shenandoah Valley Research Station
Virginia Polytechnic Institute and State University
Steeles Tavern, Virginia 24476

ABSTRACT

The limb-beating sampling method was evaluated with regard to its seasonal efficiency and the effects of the time of day of sampling. The efficiency of limb-beating was generally high throughout the season with averages of 88%, 90%, and 85% for the Salticidae, web-builder (Theridiidae and Dictynidae), and total spiders, respectively. The overall seasonal efficiency of limb-beating for the Thomisidae (includes Philodromidae) was lower (79%) due to the inefficiency in sampling early instar *Philodromus* sp. spiderlings during one sampling date. There were no significant differences ($p > 0.05$) due to time of day of sampling on population estimates obtained for the Salticidae, Thomisidae, web-builders, and total spiders during normal sampling hours of 9:00-18:00. On one of two sampling dates, more nocturnally active clubionids were collected at 3:00 than most other sample periods.

INTRODUCTION

Spiders have been indicated as important predators in Virginia apple orchards (McCaffrey and Horsburgh 1980). However, accurate population assessments are needed to further evaluate their role in the natural control of orchard arthropod pests. The conventional sampling method entails beating tree limbs with a stick over a cloth covered tray; dislodged spiders are then collected (Dondale 1958, Specht and Dondale 1960, Hukusima 1961, Legner and Oatman 1964, Dondale et al. 1979, McCaffrey and Horsburgh 1980). It is generally recognized that this sampling method is inadequate (Putman 1967, Turnbull 1960, 1973), but few studies have indicated to what extent it is deficient or the factors influencing its efficiency. With this in mind, studies were undertaken to determine: 1) the seasonal efficiency of the limb-beating technique for sampling spiders, and 2) the effect of the time of day of sampling on the population estimates obtained using this technique.

¹ Present address: Department of Entomology, University of Idaho, Moscow, ID 83843.

² Present address: Entomology Department, University of California, Riverside, CA 92521.

³ Present address: Entomology Department, Winchester Fruit Res. Lab., Virginia Polytechnic Institute and State University, Winchester, VA 22601.

METHODS AND MATERIALS

Seasonal Efficiency of Limb-beating.—This study was conducted in an abandoned apple orchard in Augusta Co., Virginia. The sample unit was the peripheral linear meter of a limb arising from the center of the tree (Lord 1965, 1968). Three limbs from each of eight 'Golden Delicious' apple trees (3-4 m tall) were sampled twice-monthly from May-August, 1977, by the conventional limb-beating method. The limbs were evenly spaced around the tree and 0.5-1.5 m from the ground. Each limb received five sharp taps with a rubber-covered stick over a 1 m² muslin covered tray; all spiders dislodged were collected, counted and identified to family. Immediately after being tapped, each limb was enclosed in a 0.88 m x 1.16 m black plastic bag, cut from the tree, and examined in the laboratory for spiders not previously dislodged. The spiders dislodged by limb-beating plus those left on the limbs were considered total capture. All limbs were tapped by the same person to reduce possible sampler variation. Individual limbs were isolated as much as possible to avoid spiders dropping down from surrounding limbs. Only a limited number of trees were available for destructive sampling; therefore, the same trees were used throughout the study. If limb removal affected the integrity of the tree, an adjacent tree was used in its place. Limb-beat and total capture population estimates were compared statistically using paired t-tests.

Effects of Time of Day of Sampling.—This study was conducted in the abandoned orchard mentioned previously. Each sample consisted of those spiders collected by beating the peripheral linear meter of 10 limbs from each of five randomly selected trees of the 'Jonathan' or 'Stayman' variety in a similar manner as described above. Samples were taken at 3 h intervals for a 24 h period 23-24 July and 21-22 August 1977. Again, spiders were identified to family. Analysis of variance and Duncan's Multiple Range Test were used to test for differences among population estimates.

Table 1.—Summary of developmental stages of selected spiders during seasonal sampling evaluation: S = spiderling, A = adult, NR = not represented.

Family, Genus, Species	Spider Stages Represented		
	May-June	July	August
Salticidae			
<i>Eris aurantia</i> (Lucas)	S	S	S,A
<i>Eris marginata</i> (Walckenaer)	S,A	S	S
<i>Hentzia</i> spp.	S,A	S,A	S,A
<i>Metaphidippus galathea</i> (Walckenaer)	S,A	S,A	S,A
<i>Phidippus</i> sp.	NR	NR	S
Thomisidae			
<i>Misumenops asperatus</i> (Hentz)	S	S,A	S,A
<i>Misumenops oblongus</i> (Keyserling)	S,A	S,A	S,A
<i>Misumenoides formosipes</i> (Walckenaer)	S	S	S,A
<i>Philodromus</i> spp.	S,A	S,A	S,A
<i>Xysticus</i> spp.	S,A	S,A	S,A
Theridiidae			
<i>Theridion</i> spp.	S,A	S,A	S,A
Dictynidae			
<i>Dictyna sublata</i> (Hentz)	S,A	S,A	S

RESULTS AND DISCUSSION

Seasonal Efficiency of Limb-beating.—Previous studies have shown that a large complex of spider species inhabits Virginia apple trees (McCaffrey and Horsburgh 1980); this was also evident during this study. A summary of the developmental stages of selected spiders encountered during the seasonal sampling evaluation is presented in Table 1.

The seasonal efficiency (spiders beat from limbs/total capture of spiders) of the limb-beating method for estimating salticid and web-building (Theridiidae and Dictynidae) populations was high with seasonal averages of 88% and 90% respectively. Also, there were no significant differences ($p > 0.05$) between limb-beating and total capture population estimates (Fig. 1). High capture efficiencies for limb-beating were expected for salticids, but not for the web-builders. Putman (1967) indicated these groups (Theridiidae and Dictynidae) to be less efficiently sampled by limb-beating, but he did not state what developmental stages he was sampling. Our observations on the behavior of mid-instar spiderlings and adults showed that when disturbed, the theridiids (*Theridion* spp.) would fold their legs close to their body and drop from their web; the dictynids (*Dictyna subulata* [Hentz]) would run along the leaf on which their web was located and jump off the edge. These behaviors would account for the high efficiencies of capture.

The seasonal efficiency of capture of the Thomisidae was generally high; however, on 12 July fifteen newly hatched *Philodromus* sp. spiderlings were found associated with one limb subsequent to beating. They were still closely associated with the silken egg sack and had not yet dispersed; they reduced the efficiency of capture to 56%. In spite of this low capture efficiency, there were no significant difference ($p > 0.05$) between limb-beat and total capture estimates (Fig. 1).

The category total spiders included representatives of the Salticidae, Thomisidae, Theridiidae, Anyphaenidae, Dictynidae, Clubionidae, Araneidae, and Oxyopidae. Again, the efficiency of limb-beating was high, averaging 85% over the season. However, there were significant differences ($p < 0.05$) noted on 19 May and 12 July between the limb-beating and total capture population estimates (Fig. 1). The overall reduction in efficiency noted on 19 May reflects a cumulative effect of reduced efficiencies for a number of spider groups including the Salticidae and the Thomisidae. The low efficiency on 12

Table 2.—Effect of time of sampling on limb-beating population estimates. Means followed by the same letter in the same column do not differ significantly ($P > 0.05$), Duncan's Multiple Range Test. Philodromids are included in the Thomisidae. Dictynids and theridiids constitute the Web-builder category.

Time	$\bar{X}$ No. Spiders/Tree									
	Salticidae		Thomisidae		Clubionidae		Web-builders		Total	
	23 July	21 Aug	23 July	21 Aug	23 July	21 Aug	23 July	21 Aug	23 July	21 Aug
6:00	3.4 bc	3.4 a	6.4 a	5.2 a	0.6 b	1.0 a	0.5 a	0.6 a	14.6 abc	13.0 a
9:00	4.6 abc	4.4 a	10.4 a	10.0 a	0.4 b	1.0 a	1.1 a	0.7 a	21.6 a	20.4 a
12:00	7.8 a	4.0 a	8.4 a	7.2 a	0.6 b	0.6 a	0.3 a	0.7 a	20.6 a	15.4 a
15:00	5.6 ab	4.6 a	10.4 a	5.8 a	0.6 b	0.8 a	0.4 a	1.0 a	22.0 a	14.8 a
18:00	5.8 ab	3.2 a	7.2 a	4.6 a	1.6 ab	0.3 a	0.6 a	0.5 a	17.8 ab	12.4 a
21:00	1.0 c	2.6 a	4.8 a	3.6 a	0.6 b	0.0 a	0.3 a	0.6 a	8.6 c	9.0 a
24:00	2.2 bc	1.6 a	4.0 a	4.8 a	1.6 ab	0.0 a	0.5 a	0.1 a	9.4 bc	8.6 a
3:00	1.8 c	2.0 a	4.6 a	2.2 a	2.8 a	0.4 a	0.2 a	0.4 a	10.8 bc	7.2 a

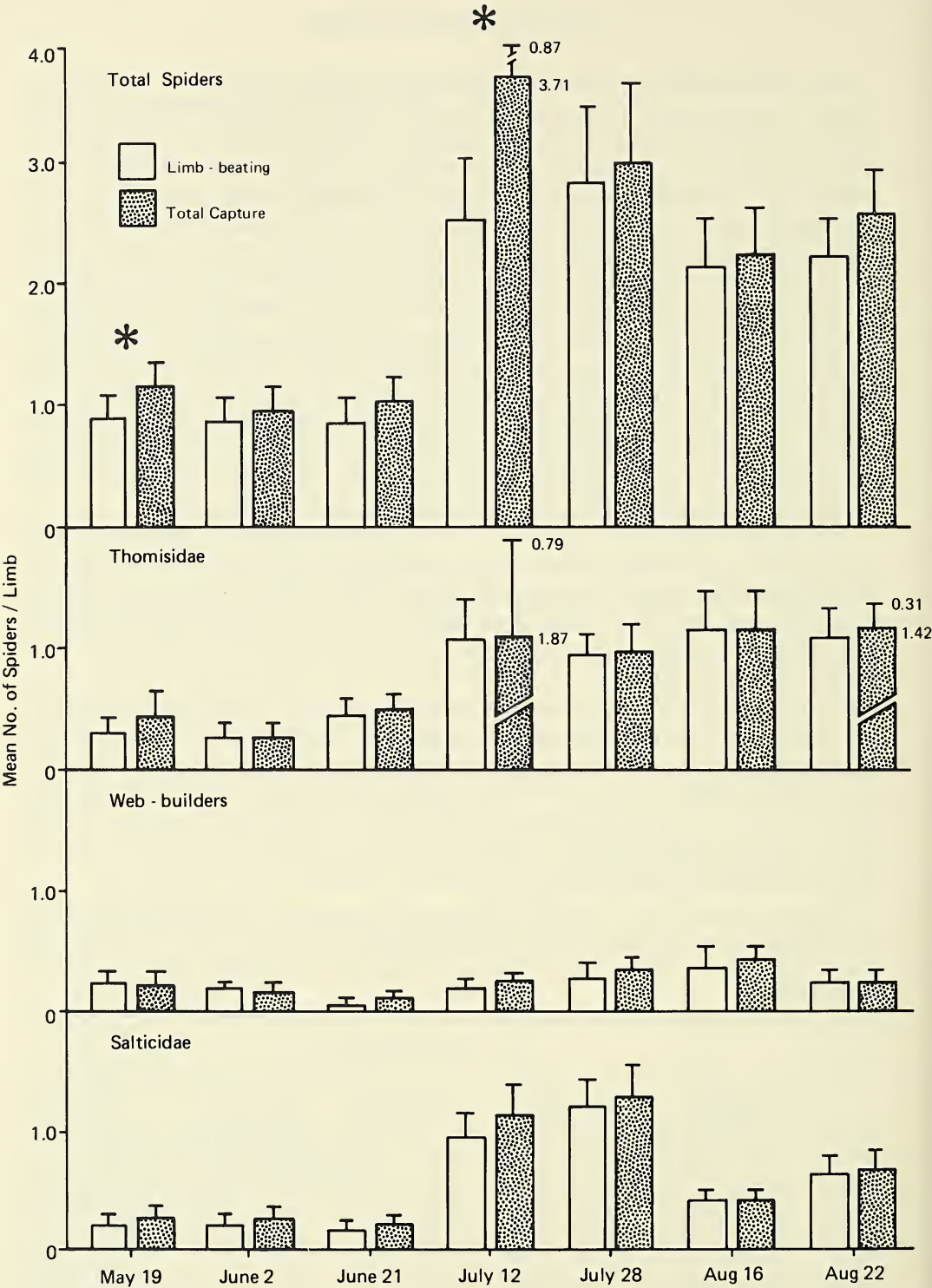


Fig. 1.—Seasonal population estimates of selected spider groups obtained using limb-beating and total capture. An asterisk indicates significant differences ($p < 0.05$) between limb-beat and total capture estimates.

July reflects the inefficiency of capturing the *Philodromus* sp. spiderlings and the cumulative small reduction in efficiencies for other families.

Effects of Time of Day of Sampling.—During July, significantly more ($p < 0.05$) salticids and total spider numbers were collected during the daytime sampling hours of 9:00-18:00 than most other sample periods (Table 2). In contrast, significantly more ($p < 0.05$) clubionids (*Clubiona* spp.) were collected at 3:00 than most other sample periods (Table 2). This was expected since the clubionids are represented by many nocturnal species. No significant differences ($p > 0.05$) were found between sampling periods for the thomisids and web-builders during July or for any spider groups in August (Table 2).

The results of this study indicate that the time of sampling by the limb-beat method has little effect on the population estimates obtained during normal sampling times, except for nocturnally active species. This supports Turnbull (1960) who indicated that this sampling method best estimates populations of those spiders active at the time of sampling; resting and hiding places are not effectively sampled.

CONCLUSIONS

The limb-beating sampling method is generally satisfactory for providing quantitative spider population estimates from apple trees. However, consideration must be given for the developmental stage of the spiders being studied; young spiderlings, for example, may not be effectively sampled. Also, the activity periods of the spiders have to be considered. Daytime sampling of nocturnally active species, such as many clubionids may not be satisfactory for estimating populations associated with trees. Finally, in this study, species groups and not individual species are considered. The compensatory actions of one species' behavior to another may have masked any true differences in spider activity and sampling efficiency. Therefore, more detailed studies considering individual species are needed to fully evaluate this sampling method.

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RESTING POSTURES OF ORB-WEAVING ULOBORID SPIDERS (ARANEAE, ULOBORIDAE)

Brent D. Opell

Department of Biology, Virginia Polytechnic Institute
and State University, Blacksburg, VA 24061

and

William G. Eberhard

Smithsonian Tropical Research Institute and
Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria "Rodrigo Facio", Costa Rica

ABSTRACT

Observations of 22 orb-weaving species of the family Uloboridae show that these spiders assume one of four basic resting postures as they hang beneath the web's hub. The primitive pattern found in *Tangaroa* and *Octonoba* is characterized by all legs being spread and about equally flexed, whereas in *Zosis* the protracted first legs grasp the web at nearly the same point. *Uloborus* species typically assume a more cryptic posture characterized by acutely protracted and flexed first legs. Dense setal tufts proximal to the abruptly flexed leg segment provide outline camouflage and conceal the extended, shorter second legs which no longer support the body. In contrast, *Philoponella* species lack leg tufts and assume a compact posture with first legs folded against the sternum and only the last three pairs of legs grasping the web. The significance of these findings for uloborid classification and phylogeny is discussed.

INTRODUCTION

We have observed species in the orb-weaving uloborid genera *Uloborus*, *Octonoba*, *Conifaber*, and *Philoponella* in the field, and *Tangaroa* in captivity. The postures they assume while hanging from the hubs of their webs during the day are generally consistent within genera and in many cases differ between them. Thus these behaviors may be useful for field identification of uloborid genera, analysis of intrafamilial phylogeny, evaluation of the family's present generic division, and understanding the functional significance of differences in morphology.

With the exceptions of studies of *Hyptiotes* (Marples and Marples 1937, Peters 1938, Wiehle 1927, Wilder 1875) and *Miagrammopes* (Akerman 1932, Lubin et al. 1978), uloborid resting postures have received little attention. This is surprising in view of the striking differences that appear in early illustrations of these spiders. For example, the

crouched posture of *Philoponella* (= *Uloborus*) *republicana* shown by Simon (1891) contrasts with extended postures of *Zosis* (= *Uloborus*) *geniculatus* and *Uloborus glomosus* (= *U. americanus*) illustrated by Comstock (1913). Wiehle (1931) illustrates comparable contrasts in the postures of *Polenecia* (= *Sybota*) *producta* and an unidentified Central American "*Uloborus*" species which, judging by its resting posture, was a *Philoponella*. Eberhard (1973) concluded that the extended posture of *Uloborus diversus* represented an adaptation for concealing the spider since it was abandoned at night when the spider rested at the hub with all eight legs spread. It is surprising to find several postures among genera that all rest at the hubs of more or less horizontal orbs, particularly when their body shape and prey capture behavior are similar.

Most specimens upon which these observations are based are deposited in the Museum of Comparative Zoology, Harvard University. Representatives of *Tangaroa*, *Octonoba*, and some *Uloborus* and *Philoponella* are in the first author's collection.

OBSERVATIONS

Although we have observed four basic resting postures, all species studied for any length of time (*U. diversus*, *U. glomosus*, *P. semiplumosa*, *P. republicana*, and *P. vicina*) show some degree of variation. For instance, *P. vicina* sometimes rested in postures A and B, but when "disturbed" usually assumed posture D. *Uloborus diversus* usually rested with legs I and II extended anteriorly and touching each other, but sometimes one or both of legs II held the web and were not in contact with the others, or one leg I was not pressed against the other. These variations were particularly common after a spider had spread its legs and jerked its web in response to the impact of a prey (i.e., had assumed posture A), then failed to completely resume its usual resting posture. Additionally, postures A and B are not always easily distinguished as they differ only in the amount of separation between the first legs. The following descriptions are thus of stereotyped, "typical" postures which spiders often but not always assumed.

Posture A.—Figures 1-4. The spider rested with all eight legs spread and partly extended with each grasping a hub thread.

Posture B.—Figures 5, 6. Legs II, III, and IV were spread and partly extended to grasp web threads. Legs I were both directed nearly straight forward to grip the web and were only slightly separated along their prolateral surfaces. Legs I were flexed only slightly at the femur-patella and tibia-metatarsus joints.

Posture C.—Figures 7, 8. Legs I and II were pressed together and extended directly forward. The tibia-metatarsus joint of legs I was held at approximately 90°, while the tibia-femur angle was relatively small (15-25°) but more variable. Legs II were held tightly against the retrolateral margins of legs I, but their metatarsi and tarsi were only slightly flexed and, instead of gripping the web, the tarsi rested together in a crypt formed by dense setal brushes on the distal surfaces of the first tibiae. Legs III and IV held the web and were held close to the abdomen.

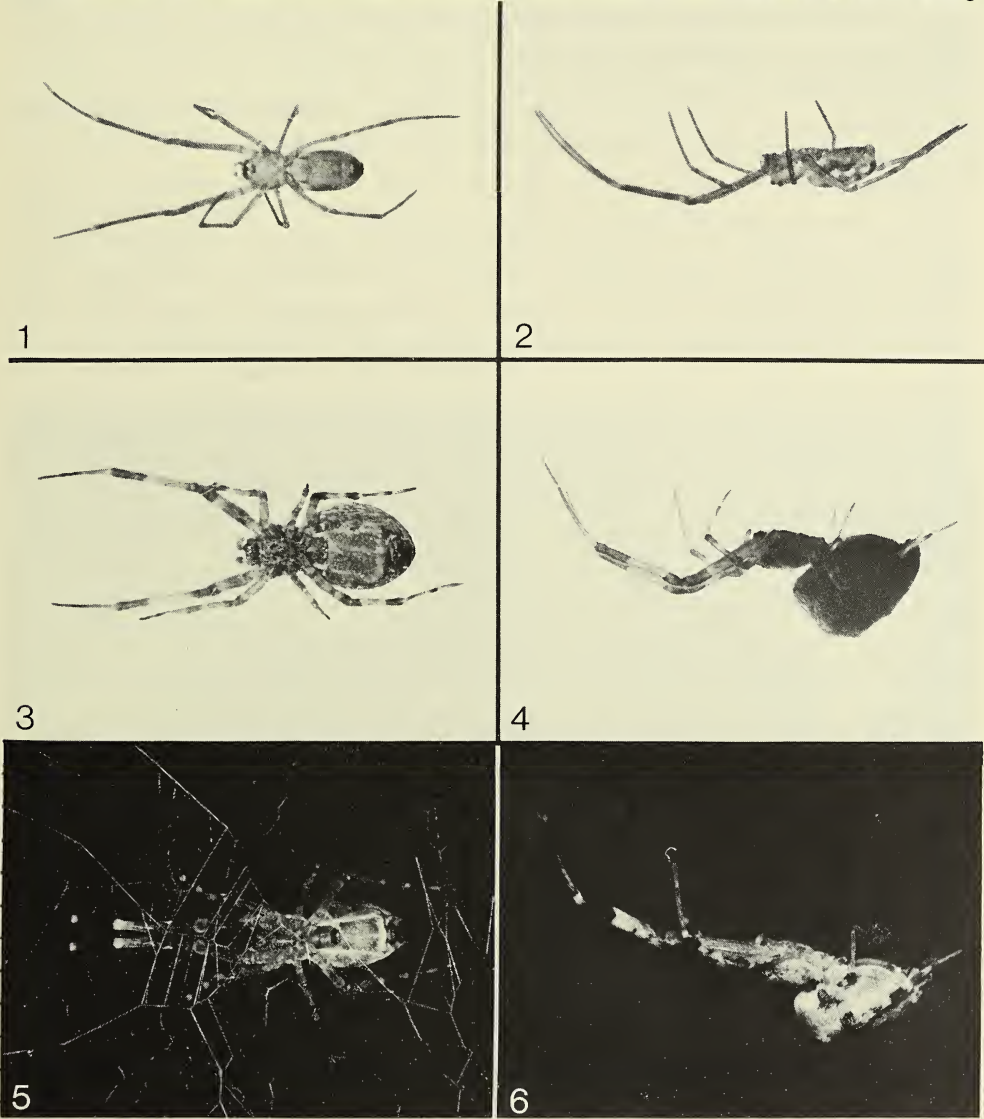
Posture D.—Figures 9, 10. The first legs were folded so that the tarsi and metatarsi were ventral to and nearly parallel with the sternum, and their tarsi did not grip the web. Legs II were also held flexed, with the femur forming a about 90° angle with the plane of the sternum; the femur-tibia angle was about 45°, the tibia-metatarsus angle about 90°, and the tarsal claws gripped the web. Legs III and IV also held the web and were pressed against the lateral surfaces of the abdomen. In at least one species (*Uloborus* 2072) the tip of the spider's abdomen projected upward and apparently pushed the web above it

into a small dome (similar behavior occurs in the araneid genera *Mangora*, *Mecynogea*, and *Cyrtophora*, but its significance is unknown).

The distribution of these postures among 22 species of orb-weaving uloborids is given in Table 1. With two exceptions (*Uloborus* 2072 and *U. conus*; Lubin et al. 1982), it appears that within a genus the resting posture is consistent.

DISCUSSION

The function of constrained postures (B, C, D) is probably one of outline concealment, serving to hide the outline of the legs and make them appear part of a single



Figs. 1-2.—*Tangaroa beattyi* Opell female: 1, ventral view; 2, lateral view. Figs. 3-4. *Octonoba octonaria* (Muma) female: 3, ventral view; 4, lateral view. Figs. 5-6. *Zosis geniculatus* (Olivier) female: 5, ventral view; 6, lateral view.

structure, thus reducing predation (e.g., Robinson 1969a). The spiders' consistent use of the relatively exposed orb hubs as resting sites (Eberhard 1969), their production of stabilimenta (thought to be camouflage devices—Eberhard 1973), the disruptive coloration of their legs (e.g., Figs. 3-12), the presence of setal brushes on tibia I of *Uloborus* species which hold legs II beside tibia I (Figs. 7, 8), and the irregular outline of the abdomens of some species (e.g., *Uloborus* 2073) are all in agreement with this crypsis hypothesis.

Four lines of evidence suggest that posture A is plesiomorphic (= ancestral) with respect to the others: 1) this is the posture of *Tangaroa*, a genus whose morphology shows it to contain the most primitive living uloborids (Opell 1979); 2) similar stances are found in other web-building spiders (e.g., Araneidae, Dictynidae, Tenggellidae, Agelenidae, and Dipluridae, personal observations); 3) this posture is assumed at night by at least some species (e.g., *U. diversus*, Eberhard 1973) and occasionally is assumed at both day and night by others (e.g., *P. vicina*) which usually adopt other, apparently cryptic postures during the day; and 4) all orb-weaving uloborids we observed assumed this posture in response to prey contacting the web when it seems to be important for prey location and evaluation.

Three morphological modifications appear to be associated with posture C: 1) Dense, distal tibial setal tufts (Figs. 7, 8) which hide the tips of the second legs, or conceal the outline of the legs, or both (perhaps equivalent to "decorations" on the legs of some mantids, walking sticks, and other insects); 2) narrowed cephalic carapace region which, at the level of the posterior lateral eyes is 0.62 maximum carapace width (mean for *U. glomosus*, *U. metae*, *U. trilineatus*), as opposed to 0.86 in *Tangaroa*, (mean for *T. tahitiensis* and *T. beattyi*), 0.77 for *Zosis*, (mean for *Z. geniculatus* and *Z. peruvianus*), 0.67 in *Octonoba octonaria*, 0.67 in *Conifaber parvus*, and 0.69 in *Philoponella* (mean for *P. fasciata*, *P. republicana*, *P. vicina*, *P. vittata*), and 3) first femora which bow retrolaterally in the proximal third of their length to accommodate their distal appression while allowing pedipalpi to extend between their bases (Fig. 7). More careful comparison will no doubt show other less conspicuous modifications that, in conjunction with 2 and 3, allow legs I to extend directly forward.

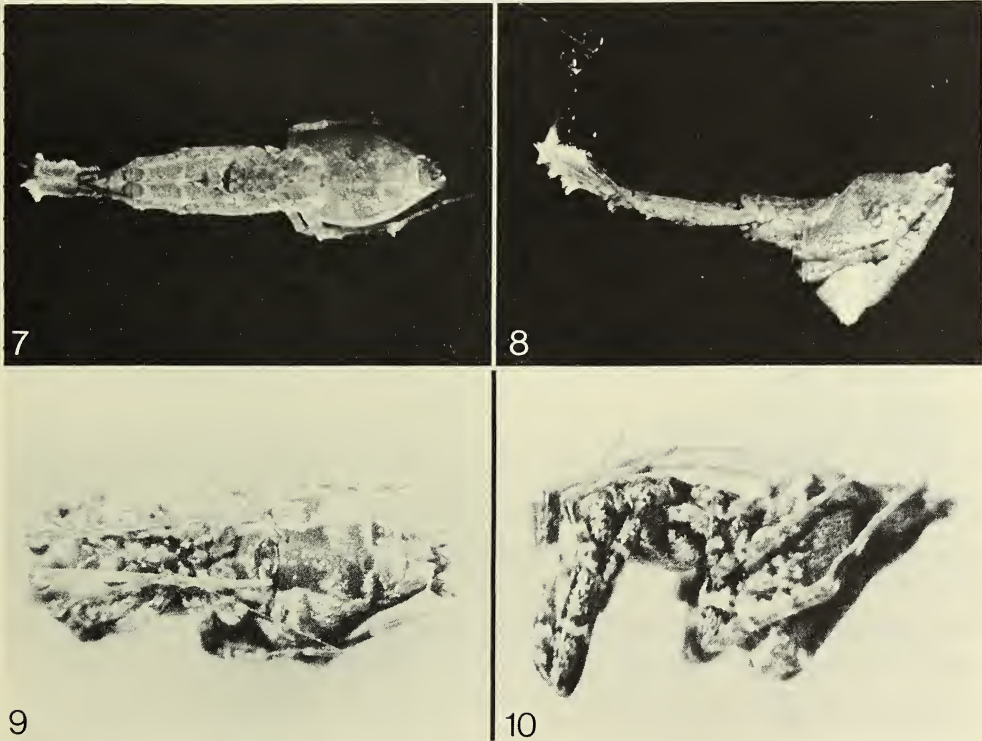
Posture C may represent a linear special protective resemblance similar to the stick mimicry attitudes assumed by some phasmids. In describing these postures Robinson (1969a, b) points out that, in addition to allowing protraction and opposition of anterior legs, adaptations similar to 2 and 3 above conceal the head and antennae, making the insects more linear in appearance. This closely parallels the situation in *Uloborus*. Although the first metatarsae and tarsae bend abruptly upward, their dark color contrasts with the lighter proximal segments and visually truncates the legs at the tibial tufts (Figs. 7, 8), maintaining a more linear appearance. In darkly pigmented *U. glomosus* the same effect is achieved by dark tibial setal tufts and light metatarsae and tarsae.

Some *Miagrammopes* species also possess distal tibial setal tufts which contribute to their cryptic appearance. It is not clear whether these tufts are homologous with those of *Uloborus*, but this would be consistent with Opell's (1979) phylogenetic proposals. Their function is probably somewhat different, however, as *Miagrammopes*' first legs are quite long and the spiders' second legs extend only to the patellae (Lubin et al. 1978, fig. 9) and, therefore, do not rest in the setal tufts as they do in *Uloborus* which rest in an extended cryptic posture. The setal tufts may obscure the outline of the first leg, but they do not hide the tips of the second legs. Perhaps this was the original function of these tufts, and their use in conjunction with posture C evolved later.

Crouched posture D contrasts with C not only because legs I and II are drawn close to the body (Figs. 9, 10), but also because legs II rather than legs I are responsible for the spider's anterior purchase on the web. Other than coloration, no morphological modifications appear to accompany this posture. In contrast to cryptic posture C, posture D may be a eucryptic device which, along with the darker color of many *Philoponella* species, renders the spider inconspicuous against its background rather than making it appear as a piece of debris. Although there is no evidence in *Philoponella* for the background selection which Robinson (1969a) lists as characteristic of eucryptic animals, *Philoponella* commonly construct webs in buttress roots of trees, on steep banks, and on rock outcrops where the background is dark. A pair of light paraxial ventral abdominal stripes usually bridge a small gap in one or more linear stabilimenta which cross the hub, further contrasting the spider and its web and helping it blend with its background.

It may be advantageous for species which are facultatively colonial, as are most *Philoponella* that have been studied (Eberhard 1969, Lahmann and Eberhard 1979, Lubin 1980, Muma and Gertsch 1964, Opell 1979), to be inconspicuous (eucryptic) rather than to exhibit protective resemblance. A number of relatively evenly spaced, suspended pieces of apparent debris might elicit further investigation by a predator and would almost certainly encourage learned recognition.

These resting postures support division of the traditional genus *Uloborus* into a number of morphologically distinct genera (Lehtinen 1967, Opell 1979) and aid in their field identification. The cryptic posture of *Uloborus* serves as an additional autapomorphic (= derived) character for most members in this genus. The more generalized posture of *Octonoba* also indicates that the *Uloborus* posture is unique to that genus and is not



Figs. 7-8.—*Uloborus trilineatus* Keyserling female: 7, ventral view; 8, lateral view. Figs. 9-10. *Philoponella vicina* (O. P.-Cambridge) female: 9, ventral view; 10, lateral view.

present in its sister group. *Zosis* posture appears derived from a generalized posture of the *Zosis*, *Octonoba*, *Conifaber* lineage. Morphological characters suggest that *Conifaber* is more closely related to *Zosis* and *Octonoba* than to *Philoponella* and its apparent postural similarity to the latter is the result of convergent evolution. Our observations of *Conifaber* were unfortunately not detailed enough to determine whether its posture is identical in every detail to that of *Philoponella*.

The occurrence of posture D in two cone-weaving *Uloborus* species (*U.* 2072 and *U. conus*) is difficult to interpret. Only brief observations were made of a single individual of

Table 1.—Daytime resting postures assumed by orb-weaving uloborids.

SPIDER	POSTURE
<i>Tangaroa</i>	
<i>beattyi</i> Opell	A
<i>Octonoba</i>	
<i>octonaria</i> (Muma)	A
<i>varians</i> (Bösenberg and Strand)	A*
<i>Zosis</i>	
<i>geniculatus</i> (Olivier) - American	B
<i>geniculatus</i> (Olivier) - Indian	B
<i>peruvianus</i> (Keyserling)	B+
<i>Uloborus</i>	
<i>diversus</i> Marx	C
<i>glomosus</i> (Walckenaer)	C+
<i>trilineatus</i> Keyserling	C & C+
<i>eberhardi</i> Opell	C
<i>segregatus</i> Gertsch	C
sp. (2073)	C
sp. (2072)	D
<i>conus</i> Opell	D**
<i>Conifaber</i>	
<i>parvus</i> Opell	D++
<i>Philoponella</i>	
<i>arizonica</i> (Gertsch)	D++
<i>oweni</i> (Chamberlin)	D++
<i>para</i> Opell	D++
<i>republicana</i> (Simon)	D
<i>semiplumosa</i> (Simon)	D
<i>tingena</i> (Chamberlin and Ivie)	D
<i>vicina</i> (O. P.-Cambridge)	D
<i>vittata</i> (Keyserling)	D

*From a photograph in Yoshida (1980). Due to variability in postures (see text), this characterization is only tentative.

+The spider held legs I and II pressed more or less together and directed forward, with III and IV close to the body, but it was not noted whether legs II held the web or not.

**Lubin et al. (1982).

++The spider definitely crouched, and its front legs were not extended anteriorly, but details of the posture were not determined.

U. 2072 and it is possible that this species may exhibit other resting postures. Both species have two morphological characters (narrow cephalic region and setal tufts on the first tibia) associated with posture C. If our functional interpretations are correct, these modifications would not evolve unless the spider already assumed a posture similar to C, so it appears that at least in this genus posture D is derived from posture C.

Thus posture D may have evolved three times in the Uloboridae: in *Conifaber*, in *Philoponella*, and in some *Uloborus* species. This apparently unattractive conclusion is nevertheless the best possible with our present data, since, if resting posture is used along with the morphological characters presented by Opell (1979), this scheme is still the most parsimonious. It is worth noting that *U. diversus* sometimes assumes a posture similar to D but with the front legs folded dorsally rather than ventrally over the cephalothorax. (fig. 3, Eberhard 1973). This posture is never used at the hub, but is sometimes assumed when the spider is alarmed and jumps from its web. It seems likely that this represents an independent derivation of the "crouching" outline which, as with posture D, hides the spider's legs.

As with many other features of uloborid biology, resting postures show striking similarities with orb-weaving spiders of the family Araneidae. The araneid *Azilia* sp. rests on its orb in a posture similar to C except that the tibial-metatarsal angle of the first leg is larger than 90°, and the spider assumes a posture similar to D after falling to the ground when disturbed.

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**SOME OBSERVATIONS ON THE INTERNAL
ANATOMY OF *DIGUETIA CANITIES* (MCCOOK, 1890)
(ARANEAE, DIGUETTIDAE)**

Andre Lopez

Laboratoire de Zoologie et Laboratoire de Pathologie comparée
Université des Sciences et Techniques, place E. Bataillon
34060 Montpellier, France

ABSTRACT

Diguetia canities (and probably other Diguettidae species also) is mainly characterized by the massive development of the poison glands, a double rostral organ, a large U-shaped coxal labyrinth, a deep prosomatic pigmentation, a group III epigastric glands, four kinds of silk glands and a new opisthosomatic structure: the supra-anal organ. These character states support Gertsch's (1958) idea linking the family with Plectreuridae between the Dysderoidea and Scytodoidea.

INTRODUCTION

The family Diguettidae is a small group of haplogyne spiders established by Gertsch (1949). It comprises only one genus, *Diguetia* Simon 1895, with about eight species (Gertsch 1958), all being restricted to America (the southwestern United States and Mexico).

The Diguettidae are cribellate Araneomorphae considered to be primitive, owing to certain characteristics of their genital anatomy, in particular the rather unspecialized epigynum and the simple copulatory bulb with an expansive spatulate conductor.

According to Gertsch (1949), the Diguettidae should be included in the section Plectruroidea, together with Plectreuridae, these two families seeming closely related by virtue of their geographical distribution, ocular area and genitalia structure. Gertsch (1958) furthermore assigns an intermediate status to Plectreuridae between the Scytodoidea and Dysderoidea. Brignoli (1978), on the other hand, integrates the Diguettidae into the Scytodoidea. The geographical distribution, biotopes and spinning-work of Diguettidae were originally studied by Gertsch (1935, 1949, 1958). Cazier and Mortenson (1962) later detailed the sheet-space composite web, the retreat ("cocoon") and feeding habits of *Diguetia canities* (McCook 1890). Lastly, prey capture and silk handling were examined thoroughly by Eberhard (1967) in *Diguetia albolineata* O. P. Cambr. However, except for a brief description of the vulva and its adnexa (Gertsch 1958), no study of internal anatomy has been performed, to my knowledge, in Diguettidae. This is why I intend to expose the main results of a general histological study of *Diguetia canities* (McCook 1890) in the present paper, thus filling the gap, describing new spider structures and attempting to establish some relationships between internal anatomy and phylogeny.

MATERIAL AND METHODS

I collected the specimens of *D. canities* (3 males, 4 females and 1 immature) in southwestern Utah, near Zion National Park, alongside the primary state road n° 15 (August 1981). In this semi-arid area, the spiders were established on *Opuntia* ("chollas" and "prickly pears" cactus), a favorite site for Diguettidae (Gertsch 1949, 1958; Cazier and Mortenson 1962).

After preservation in alcoholic Bouin's fluid, the *Diguettia* were later embedded in cytoparaffin and serially sectioned. The sections (6 μ m thick) were colored by routine staining techniques: Gabe and Martoja's triple coloration, Masson-Goldner, Groat's hematoxylin-eosin-orange G.

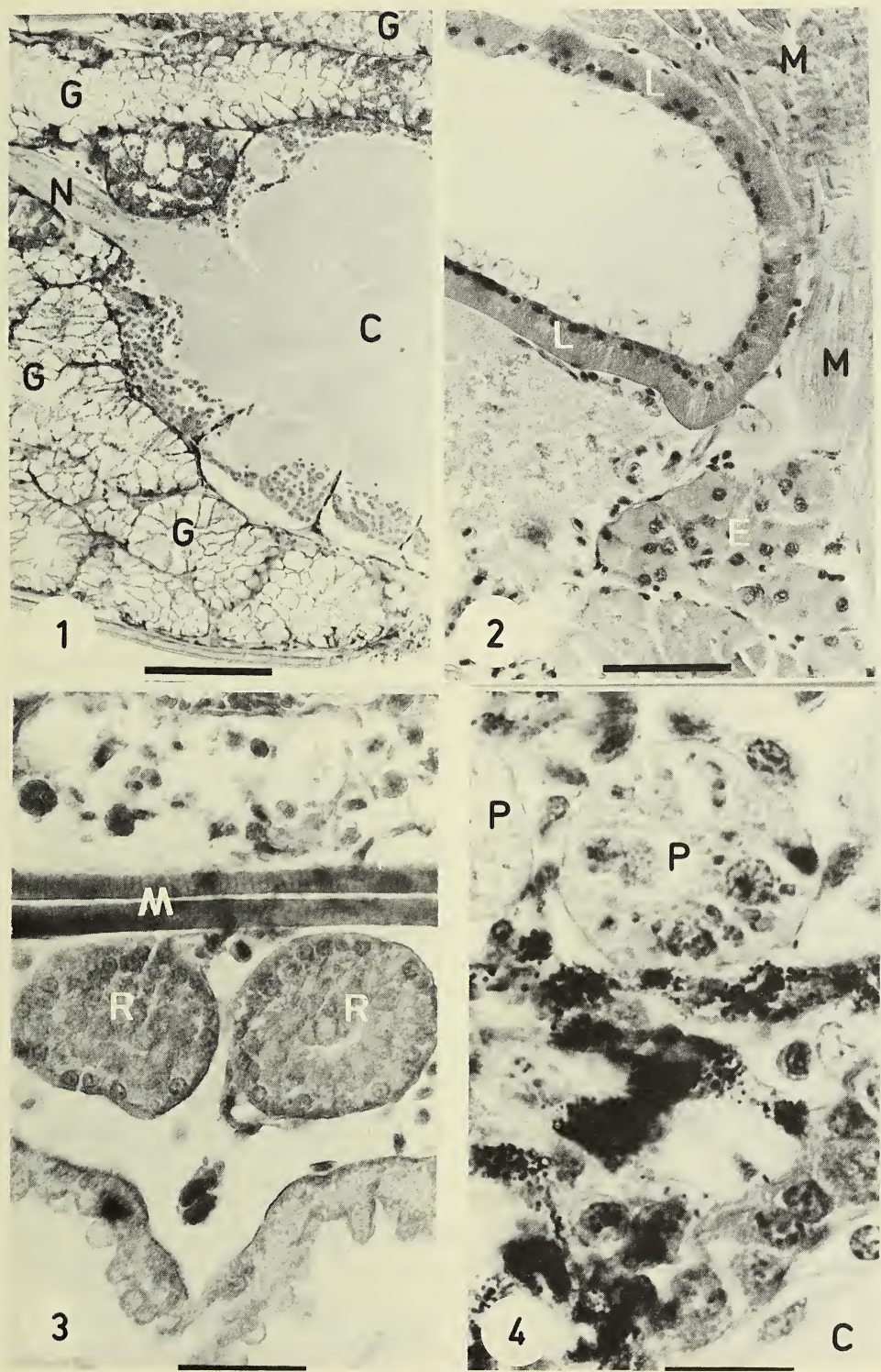
RESULTS

In the prosoma the venom glands, the coxal glands, the rostral organ, the endocrine tissue, and the male palpal bulbs were examined; pigment cells deeply located were discovered on this occasion. In the opisthosoma, the study was directed to genitalia, the male epigastric glands, the silk apparatus and the supra-anal area, which includes a new type of organ.

Venom gland.—The venom gland is remarkable for its large size, a particularly striking character of this species. The gland takes up, at least one half of the prosoma where it encloses a large part of the nervous system (Fig. 1). Ramifying in many directions the gland's pocketlike diverticula extend into the rostrum, run down along the pharynx, its so-called "taste organ" and stretch back to the cauda equina, between the suboesophageal ganglia and sternal epidermis. Except for its intracheliceral part, the gland wall, 30 μ m thick, is evenly formed in all parts by a connective sheet, a basement membrane and an inner folded secretory epithelium that surrounds a rather narrow lumen. Tall columnar prismatic glandular cells show dark staining basal nuclei and clear cytoplasm containing a small amount of a coarse granular acidophilic secretion. Muscle fibers cannot be identified beneath the basement membrane. In contrast, the intracheliceral part of the venom gland is characterized by a broader lumen and a cuboidal epithelium, just above the short venom duct. Its cells are filled with a uniformly granular acidophilic secretion.

Coxal glands.—The system of coxal glands is extremely well developed in *D. canities*. Each of the two glands includes a small sacculus facing the first leg, a conspicuous labyrinth and a short chitin-lined exit tubule, devoid of a "bladder." The labyrinth, curved into a U-shape tube, shows a prominent anterior concavity. It is formed by two, sinuous, coupled, roughly parallel limbs, one external, running backward from the sacculus, and one internal, running forward to the exit tubule. Both are mainly visible in cross sections of the prosoma. The wide lumen of each limb is bordered with an acidophilic epithelium 20 μ m high showing the usual striated cellular bases on which large clear nuclei rest (Fig. 2).

Rostral organ.—The rostral organ appears, as in other spiders, as an epidermal invagination of the anterior face of the rostrum. However, it is not a single recess but a double pocket, composed of two blind parallel tubes (Fig. 3). Moreover, the wall is devoid of the usual striated cuticular component. It is reduced to an epithelium 25 μ m thick with tall foamy cytoplasm, basal round nuclei and convex apices. The rostral cuticle remains at a distance, without invaginating into the cavities, and appears to "float" above their anterior opening.



Figs. 1-4.—*Diguertia canities*, prosoma: 1, poison gland; 2, Labyrinth of coxal gland; 3, rostral organ (cross section); 4, pigmentary cells. Abbreviations: C, cerebrum; E, endocrine tissue; G, gland; L, labyrinth; M, muscle; N, nerve; P, nephrocyte; R, rostral organ. Scale lines for Figs. 1 = 80 μ m; 2 = 60 μ m; 3 = 25 μ m; 4 = 15 μ m.

Endocrine tissue.—The endocrine tissue (Milot 1930a) or “moulting gland” (Bonaric 1980) is well represented in *Digueta* but only located in the prosoma. It appears as numerous ribbon-like or trabecular aggregations of small polymorphous cells, provided with an acidophilic cytoplasm and a vesicular nucleus (Fig. 2). These cellular islets are distributed, some laterally against the muscle and coxal glands, above the pedipalp and leg nerves, the others along the cauda equina. All associate with large nephrocytes, the cytoplasm of which includes pigmentary grains (Fig. 4).

Pigment.—This pigment, dark purplish-brown in color, is seen again in the cavities of the endochondrites, the walls of vessels and, chiefly, in the cells of the neurilemma. The latter are loaded with grains filling their poorly limited cytoplasm and concealing their clear nuclei (Fig. 4); they lie around the appendicular nerves, the cerebral mass, the suboesophageal ganglia, inclusive metameral partitions, and the cauda equina.

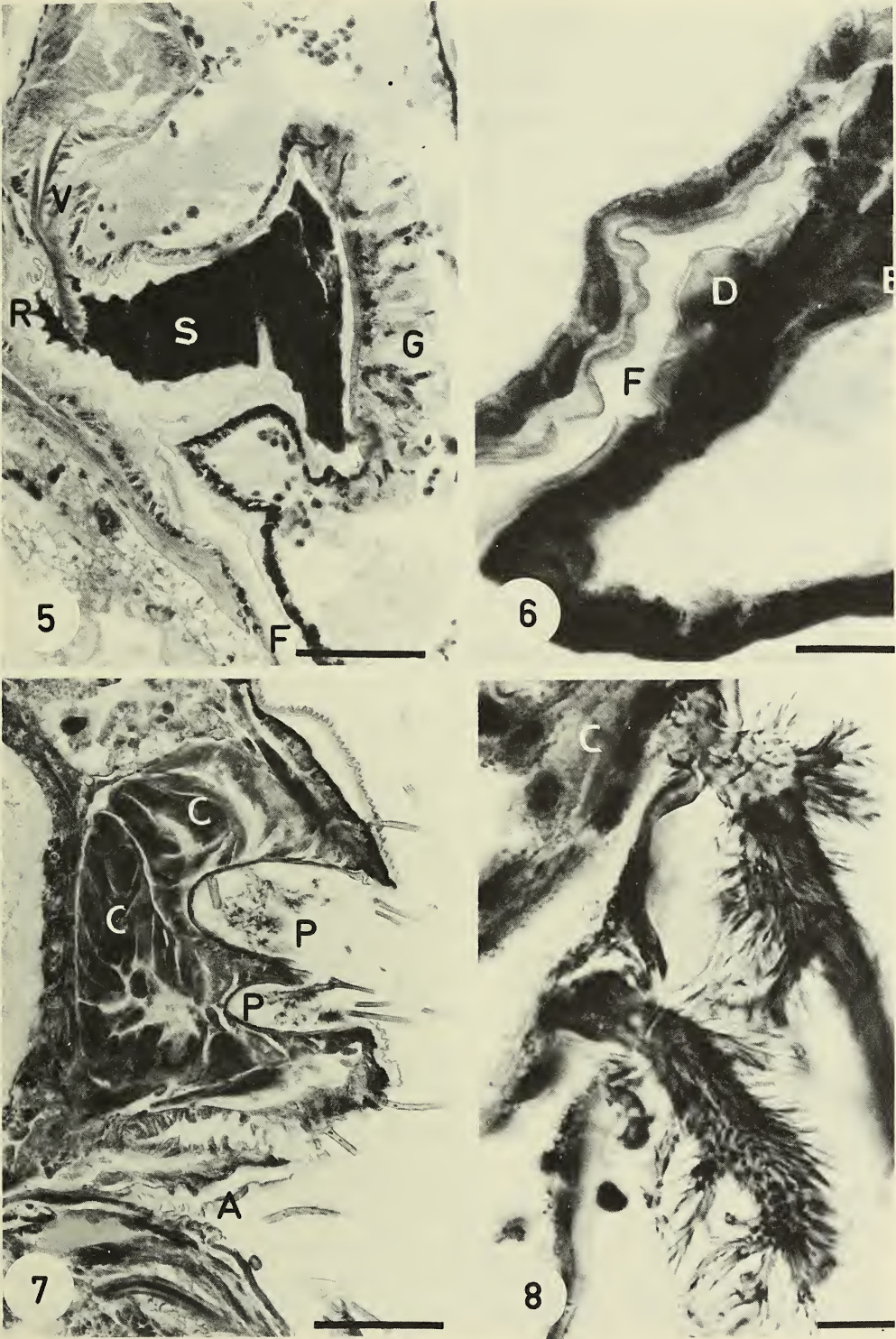
Male palpal bulb.—It includes a receptaculum seminis showing a wide lumen and a rather simple parietal structure. The fenestrate part of its cuticular wall delimits a spacious “outer palpal room” together with an adjoining basophilic secretory epithelium, the festoons of which delimit some recesses.

Female genitalia.—The female genitalia display, in the sagittal sections of their outer part all the details already outlined by Gertsch (1958:8, Fig. 17). The bursa copulatrix is wide and characterized by the presence of special glandular cells lying ventrally under its wall cuticle (Fig. 5). These cells are slender elements, 30 μ m high, arranged in convex lobules and showing a clear “combed” cytoplasm. Their separate excretory ductuli are presumably bordered with microvilli, then with duct cells and abut on tiny cups of the above-lying cuticle. Such glandular cells are lacking in the seminal receptacle, the wall of which is reduced to a cuticle and to an endotheliform flat epithelium.

Male genital tract.—This includes two long sinuous tubular testes, displaying a classical spermatogenesis, and a pair of much coiled vasa deferentia which unite at their extremities just before terminating at the epigastric furrow. The sperm cells filling the lumina are encysted individually; they do not cluster into “spermatolophids”. The anterior lip of the epigastric furrow appears devoid of the pregonoporal acinuous epigastric glands described by Lopez (1974). On the contrary, this lip includes the gonoporal type of such organs, composed of several separate unicellular glands. Each of them is provided with a tiny excretory ductulus which opens into the furrow: after crossing the pigmented epidermis, it pierces the cuticle through a small nipple-like thickening. (Fig. 6).

Supra-anal organ.—The supra-anal area is singularized by the presence of an unusual organ occurring in adults of both sexes, as well as in immature specimen. Four pocket-like tegumentary invaginations, about 120 μ m deep, open just above the anal orifice. Their modified cuticle bears ramose spiny hairs distinct from the neighbouring serrate ones. Several clusters of large chromatic cells lie beneath this cuticle. They are provided with conspicuous nuclei and gather into bag-shaped formations, apparently connected with the bases of the hairs (Figs. 7, 8).

Silk apparatus.—It comprises various glands that can be placed in four categories, according to their situation and cytological patterns and are enumerated from anterior to posterior. Category A is represented by ventral ovoid acini with short excretory ducts joining anterior spinnerets, scalloped lumen and large epithelial cells. Only belonging to one type, the latter show conspicuous nuclei and spongy basophilic cytoplasm. Category B glands are the two largest components of the silk apparatus. Their long looping ducts also open onto the anterior spinnerets. In their bodies, an ampulla and a long coiled tube can be identified; they seem to be composed of three kinds of adenocytes: one proximal,



Figs. 5-8.—*Diguertia canities*, opisthosoma: 5, female genitalia; 6, one epigastric gland; 7, supra-anal area; 8, hairs of supra-anal organ. Abbreviations: A, anus; C, cell cluster; D, ductulus near termination; E, G, gland cells; F, epigastric furrow; P, pit; R, receptaculum; S, semen; V, vaginal valve. Scale lines for Figs. 5, 7 = 60 μ m; 6, 8 = 15 μ m.

with a fine basophilic secretion; one intermediate, with a foamy cytoplasm; one distal, characterized by its plentiful spherule secretion and huge irregular nucleus. Category C glands lie between the rectum and the category B glands, and abut on the median spinnerets. They include acidophilic distal cells and intensely basophilic proximal cells, which together produce a bilayered secretion. Category D glands are also bipartite. Atrophied in the male, they show a proximal segment, with dark secretion grains, and a distal one, with clear acidophilic secretion and numerous superimposed pigmentary grains. The ducts are connected to the posterior spinnerets.

DISCUSSION

The unusual organ of the supra-anal area has apparently not been observed in any other spider. Whether it is peculiar to *Diguetia* or exists in other spiders is a question for future research. Owing to the cellular cluster connections with special ornamented hairs and the absence of evident excretory ducts piercing the cuticle of the pits, a parallel can be drawn, with the "tubes cellulaires non sécréteurs" (Millot 1931 d) or "glandes tubulaires" (Kovoor 1980) described in the basal part of *Uroctea* anal tubercle. However, the new organ of *Diguetia* is located above the anal tubercle; an integumentary fold separates it from the anal opening. In the absence of data on its fine structure, the precise function, sensorial, glandular or both, cannot yet be determined.

The occurrence of deep intracellular pigmentation is an infrequent feature, fortuitously discovered by a histological review. The single outstanding instance known elsewhere is provided by a pholcid, *Holocnemus pluchei* Scop., the pigment of which is carried by stellate cells, includes the opisthosoma and thus appears more widespread (Legendre and Lopez 1973). It is not yet possible to credit the pigment either with an active part in *Diguetia* physiology or to consider it as a superfluous metabolic waste.

The massive development of the poison glands is the most striking anatomical characteristic in *D. canities*. A similar massive venom apparatus was described previously in two other spiders: *Filistata insidiatrix* (Forsk.). (Millot 1931 a, 1949) and *Plectreurys tristis* Simon (Millot 1935). This last species displays a multilobed ramified pattern of its poison glands which similarly fill the greatest part of the cephalothorax. It also seems that *Ero aphana* (Walck.), a mimetid, possesses huge venom glands (Kovoor, pers. com.). The wide neck and its special epithelium strongly resemble the differentiations noticed in Dysderidae, Sicariidae, Palpimanidae and Pholcidae (Millot 1931 a), at least in histological sections. Given their extensiveness, the venom glands of *D. canities* probably deliver a profuse secretion, perhaps enriched with and strengthened by a product secreted by the neck. The high potency which might result from such a large volume may explain why preliminary wrapping is not required and only used to prevent loss during subsequent attacks (Eberhard 1967). An analogous correlation of extensive venom glands with an overwhelming, predominantly biting attack can be established in Filistatidae and Mimetidae (Berland 1922, Gertsch 1949, Bristowe 1958).

The coxal glands, another conspicuous anatomical feature in *D. Diguetia*, resemble strongly, by their labyrinth, the condition established as primitive by Buxton (1913) in Dysderidae and Sicariidae. They therefore become an integral part of group II, created by this author for the two other families.

The division of a rostral organ into two wholly separated blind bags has not been previously described in Araneae, although a slight bilobate pattern was noticed in various araneid species. Thus-shaped during the post-embryonic life of *Diguetia*, the double rostral organ is most interesting from the ontogenic standpoint because it appears as a

partial preservation and thus new evidence of the rostrum paired anlagen. The latter were formerly suggested by studies of nervous system development (Legendre 1959) and the discovery of cephalic coxal glands in the adults of some spider species: *Leptoneta microphthalmia* and *Metepeira incrassata* (Lopez 1978).

The endocrine tissue or "moulting gland" of *D. canities* shows a condition distinct from that noticed in primitive Araneomorphae: in the Filistatidae and Sicariidae, it is said to be non-existent, and in the Dysderidae it seems to be quantitatively reduced, in a very lateral position (Millot 1930a). On the other hand, in its abundance (more than its location) it resembles the condition in the Pholcidae.

The male genital apparatus is in conformity with the general scheme of those spiders which do not produce spermatophores. The spermatozoa are not packed into "spermatolophids" and consequently differ from the sperm cells of Dysderidae because, in the latter family, a characteristic "spherulation" occurs (Lopez 1972). The palpal bulb has an elementary histological structure somewhat resembling that of Mygalomorphae and haplogyne Araneomorphae.

The gonoporal-type epigastric glands terminate in extended order; they can be related to a new intermediate stage, that could occupy special position between group II (Dysderidae) and group IV (Pholcidae) of my original epigastric gland classification (Lopez 1974). Their secretion is probably added to the spermweb prior to induction.

The female genitalia show, in sagittal section (Fig. 5) a structure schematized by Gertsch (1958). Taking into account position and histological features, the ventral cells annexed to the bursa copulatrix can be interpreted as tiny glands that produce a sex pheromone, possibly mixed with the sperm as in other spiders (Kovoor 1982). By their strictly anteroventral location, the specialized cells of female *D. canities* differ from the dorsal cells of Pholcidae, but resemble the anterior cells of Dysderidae.

The silk apparatus shows a relatively small number of its glands. However, it tends to resemble that of more highly evolved and efficient spinners in its overall volume, as pointed out by Kovoor (1977) in Pholcidae. The complexity and size of the web that is built by *Diguetia* can thus be explained, as well as the cocoon-industry (Cazier and Mortenson 1962); on the other hand, the reduction of prey wrapping is inconsistent with the volume of the silk glands and seems to parallel, as already mentioned, poison apparatus development. It is noteworthy that some cytological features of silk producing epithelium (large size of cytoplasm and nuclei, deep basophily of certain secretions) are also encountered in the Scytodidae, Segestriidae, Dysderidae and, mainly in Pholcidae (Millot 1929, 1930^b, 1931^{b,c}).

As a result of this study, it appears that the internal anatomy of *D. canities* and probably that of the rest of the genus, displays a puzzling mix of characteristics that expresses various evolutive degrees. Some of them are undoubtedly primitive (male receptacula seminis, coxal glands, female genitalia, double rostral organ). Others seem to be more derived (endocrine tissue, silk apparatus). The evolutionary stages represented by the venom glands and the supra-anal organ are unknown. The venom gland and the female genitalia unquestionably link Diguetidae closely with Plectreuridae. Unfortunately, we know little about the other plectreurid character states, and cannot now see how extensive this linkage may be. The Diguetidae, also resemble the Filistatidae (venom glands), Scytodidae (coxal glands, silk glands), Pholcidae (venom glands, endocrine tissue, silk glands), Dysderidae and Segestriidae (silk glands, neck of venom gland, coxal and epigastric glands). Hence it follows that the family Diguetidae cannot be rigidly included in Scytodoidea; it now appears more rational to follow Gertsch's opinions (1949, 1958) which linked them with the Plectreuridae, between the Scytodoidea and Dysderoidea.

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SEXUAL DIFFERENCES IN BODY PROPORTIONS OF *ZYGOBALLUS RUFIPES* PECKHAM AND PECKHAM (ARANEAE, SALTICIDAE): AN EFFECT OF CHELICERAL AND LEG ALLOMETRY

Dean B. Faber

Department of Zoology
University of Wisconsin-Madison
Madison, Wisconsin 53706

ABSTRACT

A suspected allometric relationship between chelicera length and body size in male *Zygoballus rufipes* was investigated. In order to minimize possible effects of geographic variation, all specimens available (24 males, 46 females) from a circumscribed area in south-central Michigan were studied. Power curve regressions of carapace width, carapace height, chelicera length, palp length, first leg length, and second leg length on a general measure of body size (carapace length) were calculated for each sex. The allometric relationship was expressed as $Y = b X^k$. In females all body measurements varied isometrically (linearly) with respect to carapace length ($k = 0.91 - 1.04$). In males chelicera length and first leg length were positively allometric with respect to carapace length ($k = 1.43$ and 1.44 respectively). The other male body measurements were all isometric with respect to carapace length ($k = 0.96 - 1.04$), with the exception of carapace width which was negatively allometric ($k = 0.84$). Tests of significance for differences between sexes in the slopes of the regression lines demonstrated significant differences for chelicera length ($p < 0.10$) and first leg length ($p < 0.02$). The allometric relationships of chelicera length and first leg length with carapace length in male *Z. rufipes* demonstrate a size dependent difference between sexes in body proportions (allomorphy). This allomorphy explains why sexual dimorphism is more pronounced among larger individuals of *Z. rufipes*.

INTRODUCTION

The term allometry encompasses a variety of different phenomena. Perhaps the most succinct recent definition is that of Gould (1977):

"allometry: change of shape correlated with increase or decrease in size. The change in size may reflect ontogeny, phylogeny, or merely the static differences among related individuals. . .".

A brief introduction to allometry is presented in Futuyma (1979). For more detailed discussions see Rensch (1960), Gould (1966, 1977), and Huxley (1972).

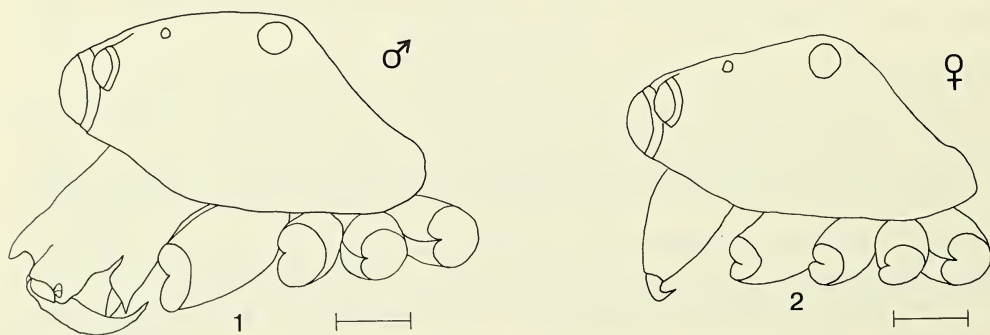
The present study is concerned with the variation within populations of adults of *Zygoballus rufipes* Peckham and Peckham and is a study of "... the static differences among related individuals. . .". This area of allometry has been variously referred to as allomorphy (Simpson 1953, Gould 1966, 1977), size allometry (Mosimann 1970), and allometrie de taille (Teissier 1960). *Zygoballus rufipes* Peckham and Peckham 1885 is the senior synonym of *Zygoballus bettini* Peckham and Peckham 1888 (Edwards 1980).

Studies of size allometry (allomorphy) in arthropods have been confined almost exclusively to the Insecta and Crustacea (see Oster and Wilson 1978, and Teissier 1960 respectively for detailed accounts). Within the Chelicerata, size allometry in Pycnogonida is discussed by Fry (1964) as an important complicating factor in numerical taxonomic analyses. Fisher (1977), based on experimental studies with models, concludes that prosomal spine allomorphy in the carboniferous xiphosuran *Euproops danae* minimized lateral oscillations during settling behavior and thereby helped the animals to escape from predators. In addition Locket (1932, cited in Huxley 1972) reports on studies of chelicerallometry in three species of spiders: *Theridion lineatum* and *T. instabile* (Theridiidae) and *Linyphia triangularis* (Linyphiidae). All three species show a positive chelicerallometry in males and either isometry or a slight negative chelicerallometry in females.

One of the distinguishing and frequently noted characteristics of the jumping spider genus *Zygoballus* is the presence of large, forward-directed chelicerae in males (Fig. 1, Peckham and Peckham 1909, Chickering 1944, Kaston 1948, 1978). Female *Zygoballus* have moderate-sized, downward-directed chelicerae (Fig. 2) such as are typical of both sexes in the great majority of Salticidae. This sexual dimorphism in the chelicerallomorphology of *Zygoballus* is present only in adults. The characteristic chelicerae of the male are acquired at the final molt to maturity (Peckham and Peckham 1909). Chelicerall sexual dimorphism occurs in other salticid genera, of which *Salticus* and *Eris* are perhaps the best known examples (Kaston 1948). In addition to the enlarged chelicerae typical of the entire genus, the males of *Z. rufipes* also have much longer first legs relative to their overall size than do the females of this species (Peckham and Peckham 1889, 1909, Emerton 1891, Chickering 1944).

I am currently engaged in a revision of *Zygoballus* for the world. The examination of many specimens of *Z. rufipes* revealed that there was little sexual difference in chelicera and first leg length among small individuals of the same body size. However, among large individuals, males had disproportionately longer chelicerae and first legs than females of the same body size. Hence, allometric relationships between chelicera length and body size and between first leg length and body size were suspected.

The present study investigates the chelicerae, palpi, first and second legs, carapace width, and carapace height in both sexes of *Z. rufipes* for allometry with respect to carapace length. Carapace length was chosen as a general measure of body size because it is the largest linear dimension of the body which can be measured accurately. Total body length was not used because of the well known tendency of the abdominal dimensions of spiders to vary with the nutritional state of the individual.



Figs. 1-2.—*Zygoballus rufipes* lateral views of the carapace: 1, male; 2, female. Scale lines equal 1 millimeter.

Table 1.—Descriptive statistics for seven body dimensions of *Zygoballus rufipes*, measured in millimeters.

		mean	standard deviation	coefficient of variation	range
carapace	males	4.55	0.60	0.13	3.41 - 5.55
length	females	4.29	0.25	0.04	3.84 - 4.89
carapace	males	4.00	0.47	0.12	2.99 - 4.76
width	females	3.72	0.23	0.06	3.29 - 4.45
carapace	males	2.79	0.37	0.13	1.95 - 3.41
height	females	2.40	0.17	0.07	2.13 - 2.74
chelicera	males	2.46	0.50	0.20	1.46 - 3.17
length	females	1.52	0.16	0.10	1.03 - 1.83
palp	males	4.83	0.72	0.15	3.54 - 5.85
length	females	3.70	0.30	0.08	3.23 - 4.39
first leg	males	16.83	3.31	0.20	9.81 - 22.20
length	females	10.85	0.78	0.07	8.90 - 12.56
second leg	males	9.92	1.41	0.14	6.04 - 11.58
length	females	8.35	0.63	0.07	7.07 - 9.69

In order to minimize the possible effects of geographic variation, the largest sample available from a single circumscribed geographical area was used (46 females and 24 males from an area in south-central Michigan).

MATERIALS AND METHODS

Specimens.—The specimens of *Z. rufipes* used in this study (24 males and 46 females) were collected from nine different localities in south-central Michigan. All specimens are adults collected by Arthur M. Chickering during 1930-1949 and are in the collection of the Museum of Comparative Zoology (MCZ). The collection localities all fall within a rectangle centered on Albion, Michigan and measuring 125 km. east to west and 55 km. north to south. The earliest day of the year of the nine different collection dates is April 27 and the latest is December 7.

Measurements.—Seven body dimensions of each spider were measured at 40x with an ocular micrometer (measurements of bilateral structures were made on the left side of the body). The body dimensions measured were: carapace length, maximum carapace width, maximum carapace height, chelicera length (measured from point of emergence from the carapace and not including the fang), palp length (less palpal coxa and trochanter), total first leg length (all seven segments), and total second leg length. Palp length, first leg length, and second leg length were sums obtained by adding individual limb segment lengths. The manner in which the carapace margin overlaps the insertions of the chelicera and palp makes it impossible to measure their total length without dismembering the specimens.

Statistical methods.—Descriptive statistics of the body dimensions (mean, range, standard deviation, and coefficient of variation) were calculated separately for each sex. After a logarithmic transformation, least squares linear regressions of the logs of each of the other six body dimensions on log carapace length were calculated for each sex. Linear

Table 2.—Allometric regression of coefficients of *Zygoballus rufipes* for X and Y measured in millimeters where X = carapace length and $Y = bX^k$. p = level of significance of the differences between sexes in the slopes (k values) of the regression lines.

Y		k	p	b	r
carapace width	males	0.84	>0.15	1.12	0.96
	females	0.94		0.94	0.87
carapace height	males	0.96	>0.50	0.65	0.94
	females	0.91		0.64	0.73
chelicera length	males	1.43	<0.10	0.28	0.90
	females	1.04		0.33	0.55
palp length	males	1.04	>0.50	0.99	0.93
	females	0.97		0.90	0.69
first leg length	males	1.44	<0.02	1.88	0.91
	females	1.01		2.49	0.80
second leg length	males	1.04	>0.50	2.03	0.92
	females	0.95		2.10	0.73

correlation coefficients were also calculated using the transformed measurements for each of the other six body dimensions and carapace length. Tests of significance were performed for differences between sexes in the slopes of the regression lines for each body dimension regressed on carapace length. All of the above methods are discussed in detail in Steele and Torrie (1981).

RESULTS

Descriptive statistics for each of the seven body dimensions measured are shown in Table 1 and summarized graphically in Fig. 3. The mean, standard deviation, coefficient of variation, and range are larger in males for every body dimension studied. Note that the coefficients of variation for chelicera length and first leg length in males are particularly large.

The allometric regression coefficients and correlation coefficients for all regressions are shown in Table 2. In the females all body dimensions measured vary isometrically (linearly) with carapace length, with k values between 0.91 and 1.04. In the males chelicera length and first leg length vary with carapace length in a positively allometric fashion, with k values of 1.43 and 1.44 respectively. Carapace width, however, varies with carapace length in a negatively allometric fashion with a k value of 0.84. The other male body dimensions all vary isometrically with carapace length with k values between 0.96 and 1.04. A comparison of the allometric relationships for chelicera length for both sexes is shown graphically in Fig. 4. The results of tests of significance for differences between sexes in the slopes of the allometric regression lines are shown in Table 2. The slopes for regression lines are also shown in Table 2. The slopes for regressions of chelicera length and first leg length on carapace length are significantly different between sexes at $p < 0.10$ (one tailed). The slopes for the other regressions are not significantly different between sexes, although those for carapace width are nearly significant at $p = 0.10$.

DISCUSSION

The presence of size allometry (allomorhosis) with respect to carapace length in the chelicera length and first leg length of male *Zygoballus rufipes* has been demonstrated in the sample studied. Tests of significance for sexual differences in the slopes of the allometric regressions of chelicera length and first leg length on carapace length indicate that the differences in the body proportions of larger members of the two sexes are a consequence of isometry in females and positive allometry in males.

While calculating the regression data for this study, I observed that the males collected during the summer months of July and August were consistently larger (as measured by carapace length) than those collected in either the spring (May and June) or fall (September and October). No such differences were apparent in females. This lead me to question whether there was a seasonal component to allometry in *Z. rufipes*. This hypothesis has been verified (Faber, in preparation).

The reasons for these sexual differences have not yet been clarified. The acquisition of enlarged chelicerae and first legs in male *Z. rufipes* at the final molt to maturity would suggest that male cheliceral and first leg allometry are connected with courtship display, male threat display, or some other aspect of adult behavior.

The Peckhams (Peckham and Peckham 1889) reported that two males of *Z. rufipes* "... displaying before one female rushed savagely upon each other and fought for 22 minutes, during one round remaining clinched for six minutes." Rovner (1969) reports similar behavior in *Linyphia triangularis*. Enlarged chelicerae would confer an obvious advantage in these "jousts."

In male *Z. rufipes* the first pair of legs are held above and to the sides of the body during courtship and threat displays (Peckham and Peckham 1889). It is possible that disproportionately long first legs may increase threat display and courtship success. If this is the case, then male cheliceral and first leg allometry would be consistent with Huxley's energy budget hypothesis (Huxley 1972). There may be a minimal total amount of energy required for a male to complete the life cycle. Beyond this amount however, reproductive success may be maximized by the allocation of as much energy as possible to the development of structures used in courtship and threat displays.

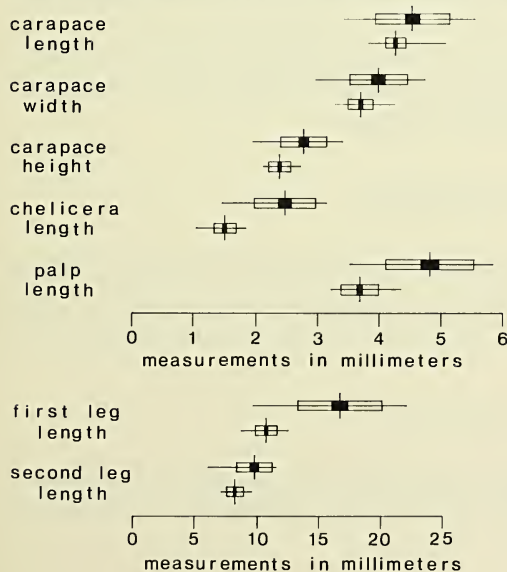


Fig. 3.—Graphical representation of descriptive statistics for all body dimensions measured for both sexes of *Zygoballus rufipes* (measurements in millimeters). The upper of each pair of symbols is for males, the lower is for females. Vertical line signifies means, horizontal line signifies range, unshaded bar signifies standard deviation, shaded bar signifies standard error of means.

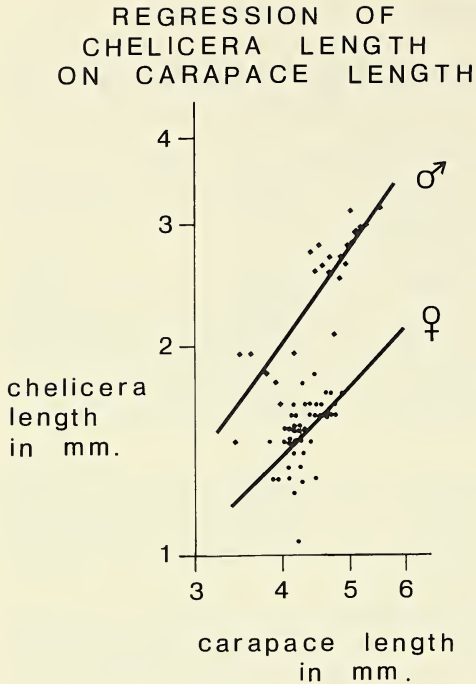


Fig. 4.—Plot of the regressions of chelicera length on carapace length for both sexes of *Zygoballus rufipes*. Males designated by diamonds, females by circles.

If fertile females are available for mating at all seasons, it may be that during periods of relative abundance of food, large males with disproportionately long chelicerae and first legs are more successful in mating with females, but during periods of food shortage there is little energy that can be allocated to the development of long chelicerae and first legs.

The presence of positive cheliceral allometry in *Zygoballus rufipes* males increases to three (Salticidae, Theridiidae, and Linyphiidae) the number of spider families in which this phenomenon is known to occur. The hunting methods of *Zygoballus* are considerably different from those of *Linyphia* or *Theridion*. The presence in adult males only of positive cheliceral allometry in such phylogenetically distant and morphologically different families would suggest that there is a selection for this phenomenon which is independent of hunting strategy. Enhanced success in intermale aggressive display and fighting and consequent enhanced reproductive success may be the common factor selecting for positive cheliceral allometry in these three genera of spiders.

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CHARACTER VARIATION IN THE SCORPION
PARABUTHUS VILLOSUS (PETERS) (SCORPIONES, BUTHIDAE):
A CASE OF INTERMEDIATE ZONES

Alexis Harington

Department of Zoology, University of the Witwatersrand
1 Jan Smuts Avenue
Johannesburg 2001, South Africa

ABSTRACT

The scorpion *Parabuthus villosus* (Peters) shows variation in leg colors over its range. The distributions of the color morphs are parapatric. A fairly narrow intermediate zone is found where the yellow and black legged morphs meet. A similar zone is present at the parapatric interface between *P. villosus* and *P. brachystylus*. Using multivariate morphometrics the morphological variation was found to be insignificant between the color morphs, but intermediates between *P. villosus* and *P. brachystylus* show morphology in-between that of the presumed parental forms. Factors that may be involved in the maintenance of the step lines are also suggested. Finally, *P. brachystylus* is given subspecific status.

INTRODUCTION

The scorpion *Parabuthus villosus* (Peters) is a large buthid widespread in Namibia. It differs from other members of the genus in that it is partly diurnal (Newlands 1974, Harington 1982). The species is characteristic of dry rocky habitats in Namibia and the northwestern Cape Province of South Africa. It does not occur in the sand dune areas of the Namib and Kalahari Deserts proper, but is sometimes found in places where dunes and rocky hills run together. It is a rupicolous species, sheltering under stones, where scrapes are sometimes constructed. Currently, *Parabuthus brachystylus* Lawrence is considered to be most closely related to *P. villosus* and is found predominantly in the northern third of Namibia (Lamoral 1979). This scorpion occurs in similar habitats to those described for *P. villosus*.

In spite of the large range occupied by *P. villosus*, little morphological variation is noticed. In contrast, there is considerable variation in the colors of the legs and pedipalps. In the present contribution the nature of this variation in *P. villosus* is analysed and the relationship between *P. villosus* and *P. brachystylus* is investigated.

METHODS

Collection of specimens was done manually by turning over rocks, and by the use of ultraviolet lamps in the summer months. In spite of the wide distribution of *P. villosus*, it

is not easy to find. To supplement the specimens collected, all available preserved material of *P. villosus* and *P. brachystylus* in South African and Namibian museums was examined.

Because the morphological differences among the color variants and between *villosus* and *brachystylus* are not marked, a multivariate morphometrical method was employed to assess the importance of various characters. About 150 adults were available for the multivariate analysis. Fifteen measurements per specimen were made using an ocular micrometer. As the *Parabuthus* cauda contains a wealth of taxonomical characters most measurements were taken there. The length and width of the caudal segments (including the telson), the length of the stridulatory patch on caudal segment two, and the lengths of the first and fourth patellae on the right side of the scorpion were measured. Width, being the maximum distance between the bases of the median lateral keels, was measured dorsally. Length, as the minimum distance between the condyles, was measured dorsally, and the width of caudal segment five taken ventrally as the maximum distance between the bases of the ventrolateral keels. The landmarks used are illustrated in Fig. 1. Assignments to color classes was not particularly difficult since the color is largely stable in preservation and ontogeny.

Direct micrometer readings were used as data for computer analysis. One micrometer unit was equivalent to 0.15 mm. In the discriminant analysis, a Statistical Package for the Social Sciences program (see Klecka 1975) was used and run on an IBM 37T/158 computer.

COLOR VARIATION IN *PARABUTHUS VILLOSUS*

Color variation in scorpions is well known and fairly common (see Lamoral 1979, Williams 1970, 1980). Before describing it in *P. villosus* it is useful to consider its nature as known in other scorpions. Generally color differences are of an intraspecific nature.

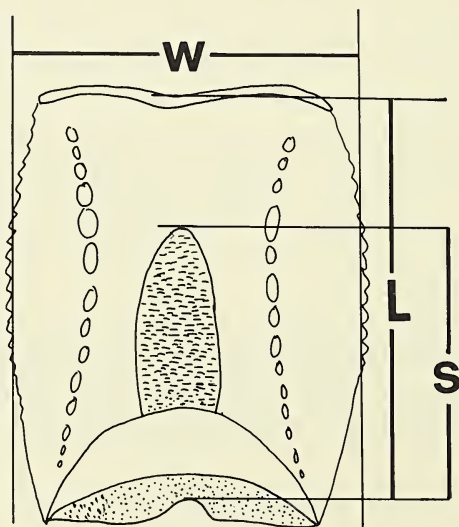


Fig. 1.—Reference points used for measurement of metrical parameters of the cauda of *Parabuthus*. Dorsal view of caudal segment 2 illustrated. *w*, *l*, and *s* indicate width of caudal segment, length of caudal segment, and length of stridulatory patch respectively.

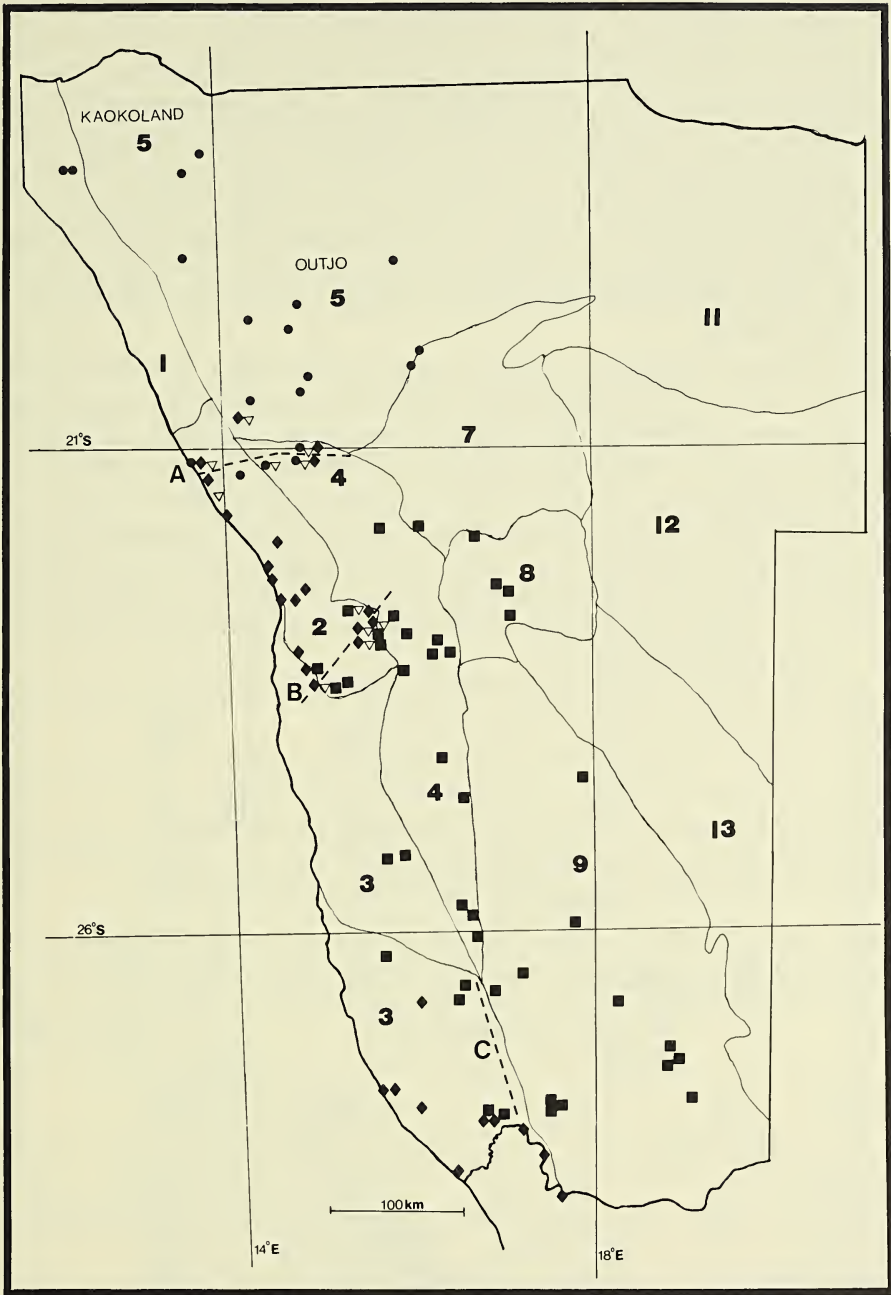


Fig. 2.—Map showing distributions of the color morphs of *Parabuthus villosus* and *P. brachystylus* superimposed on vegetation zones. Note correlation of distributions of scorpions and location of the intermediate zones with vegetation. Scorpions: dots—*brachystylus*; northern triangles—*villosus-brachystylus* intermediates; northern diamonds—black morph; southern triangles—color intermediates; squares—yellow morph; southern diamonds—southern black morph. Intermediate zones: A, *villosus brachystylus*; B, Central; C, Southern. Vegetation: 1—Northern Namib; 2—Central Namib; upper 3—Southern Namib; lower 3—Desert and Succulent Steppe; 4—Semi-desert and Savannah Transition; 5—Mopane Savannah; 7—Thornbush Savannah; 8—Highland Savannah; 9—Dwarf Shrub Savannah; 11, 12 and 13—Kalahari Savannahs.

One form of color difference reported is a type of polymorphism. In *Centruroides exilicauda* (Wood) various color morphs are sympatric and produced from the same broods (Stahnke 1971, Williams 1980). A second type of variation is the formation of local races. This class includes most of the color differentiation commonly encountered. In the South African turf scorpion, *Cheloctonus jonesi* Pocock, leg color varies from black to bright yellow and intermediate colors are common. In this scorpion variants do not usually occur sympatrically but form several races over the distribution of the scorpion. Similar race formation is reported from *Hadrurus concolorous* Stahnke and *Nullibrotheas allenii* (Wood) (Williams 1980). Many scorpions of the genera *Buthotus*, *Parabuthus*, *Uroplectes*, *Hadogenes* and *Opisthophthalmus* show color variations (see Lamoral 1979) which would fall into this category.

Color variation in *Parabuthus villosus* falls into a third class. The type of situation encountered here is not common and the best and possibly only example reported is that discussed by Williams (1970, 1980). Two subspecies of *Hadrurus arizonensis* Ewing are involved, one *H. a. arizonensis* (Ewing) is dark olive in color and another, *H. a. pallidus* Williams is yellow. The former subspecies is mainly distributed in the Sonoran desert and the latter largely in the Colorado desert. Where their distributions meet, a swarm of intermediates exists representing parentals, and all degrees of intergrades. These are apparently produced by hybridization (Williams 1970, 1980). A similar situation is presented by *P. villosus*. Four color categories can be distinguished. All have dark blackish brown to black trunks and cauda:

1. Black morph.—Black to dark brown legs and pedipalps. Little or no contrast between appendages and trunk. Occurs in northern Namibia.
2. Yellow morph.—Bright yellow to yellow legs, brown to yellow pedipalps. Appendages - body contrast marked. Found in central and southern Namibia.
3. Southern black morph.—As in 1, but confined to the southwestern corner of Namibia.
4. Intermediates.—Leg and pedipalp colors represent a complete range of intermediates between 1 and 2. They are present within a restricted geographical area.

Table 1.—Group means and standard deviations for each morphometric measurement of yellow morphs and black morphs in micrometer units (1 micrometer unit = 0.15 mm).

Variable	YELLOW MORPH		BLACK MORPH	
	Mean	S.D.	Mean	S.D.
Length cauda 1	51.79	5.04	53.94	4.66
Width cauda 1	48.75	4.97	51.72	4.47
Length cauda 2	58.68	5.74	61.06	4.83
Width cauda 2	47.00	4.28	49.72	3.94
Stridulatory length	41.29	4.43	43.58	3.40
Length cauda 3	59.43	6.12	61.94	4.67
Width cauda 3	46.32	4.04	48.72	3.59
Length cauda 4	64.50	6.21	67.28	5.05
Width cauda 4	44.64	3.88	47.39	3.85
Length cauda 5	66.57	6.31	69.17	5.06
Width cauda 5	38.14	3.74	41.06	3.59
Length telson	83.99	7.74	85.88	7.03
Width telson	41.19	5.27	44.67	5.25
Length patella 1	43.79	3.38	45.00	2.74
Length patella 4	71.36	6.18	74.39	5.18

The color variations described above are peculiar because the distribution ranges of the first, second and third morphs are largely allopatric and intergradation occurs over narrow zones. It is very unusual to find a particular morph within an area characteristic of another. The yellow morph occupies the widest range and occurs from the northwestern Cape throughout the central Highlands with the northernmost record being the farm Krantzberg 59, Karibib district. In the southwest the yellow morph is replaced by the southern black morph which is characteristically found in the very arid Diamond Area 1. In the west central area the yellow morph is replaced by the black morph. This latter extends from this area to the southern part of Damaraland (approximately 21°20'S) where it is replaced by *P. brachystylus*. Fig. 2 shows the basic distribution pattern described here.

The most relevant regions for the study of these color variations are the zones of intergradation. Two such zones exist and these are discussed below.

Central zone.—This zone resulting from intergration of the black and yellow morphs is located within the Namib Desert Park. The belt is narrow (about 40 km wide) and a complete spectrum of intermediates occur mainly within the area demarcated by a line connecting Gobabeb, Ganab, the Tinkas Mountains and Swartbank (Fig. 3). It is important to notice that both parental forms and the color intermediates are sympatric at Gobabeb, a locality in this zone. Here the yellow morph, intermediates and black morph comprise 45, 30 and 25 per cent of the population respectively (n = 40).

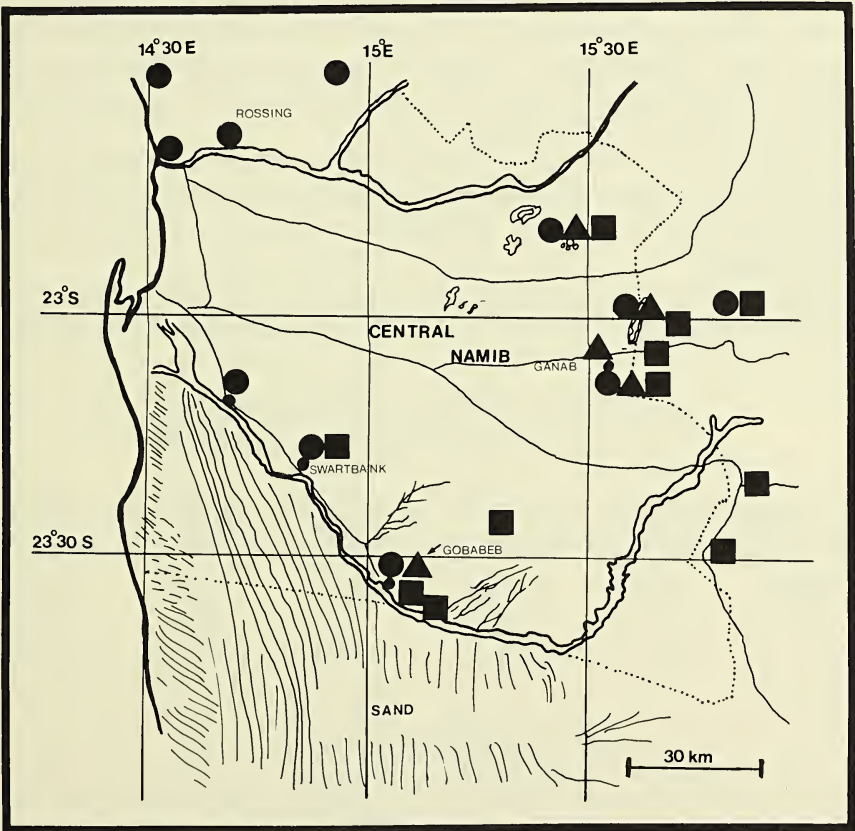


Fig. 3.—Map of Central Namib desert showing location of the central intermediate zone. Squares represent the yellow morph, dots the black morph and triangles color intermediates.

Southwestern zone.—This area is located along the eastern border of Diamond Area 1. At one locality, the farm Tsiub 13, Lüderitz district, the yellow morph and the southern black morph are sympatric but no intermediates have been found. Here the black/yellow transition is abrupt. At a second known locality of sympatry (Rosh Pinah - Namuskluft 88), much further south, intermediates are present. Due to lack of material the southwestern zone is too poorly known to allow much further analysis.

As the color variants already described are largely allopatric it was decided to investigate whether any morphological differences exist between the morphs. Twenty scorpions from Rössing Uranium Mine (black morph) and twenty from Gobabeb (yellow morph) were used in the multivariate analysis. These sample sizes are fairly large and the localities relatively close. Discriminant function analysis involves the simultaneous analysis of several variable characters and is one of the most sensitive methods known for separating groups on the basis of morphology. After measurements have been taken, a discriminant function is derived from them. This is a complex procedure involving the calculation of vectors and weighting coefficients for each particular variable. These discriminant functions express the differences between the groups in terms of a few common gradients of variation rather than all the possible gradients. The functions are designed to maximise group separation and make these as statistically distinct as possible. More detailed explanation of the theory behind multivariate discriminant function analysis is provided by Klecka (1975).

Results.—Table 1 gives the group means and standard deviations. In the discrimination process the width of caudal segment 5, the width of the vesicle and length of the vesicle were used in the discriminatory procedure. The standardised discriminant function coefficients for these three characters were respectively: 1.547, 1.088 and -2.215. The last character was the best discriminating variable.

As is apparent from the frequency histogram (Fig. 4), separation of black morphs was not successful and a large degree of overlap exists. Thus on the basis of the characters studied here, it can be concluded that no significant morphological differences are present between the morphs.

Before discussing in detail the significance and causes of the intergradation zone already described, the relationship between *P. villosus* and *P. brachystylus* will be dealt with.

ANALYSIS OF THE *PARABUTHUS VILLOSUS* AND *BRACHYSTYLUS* INTERGRADATION ZONE

The scorpion *Parabuthus brachystylus* Lawrence was described from localities far north of the then known distribution of *P. villosus*, being taken in the Kaokoveld and

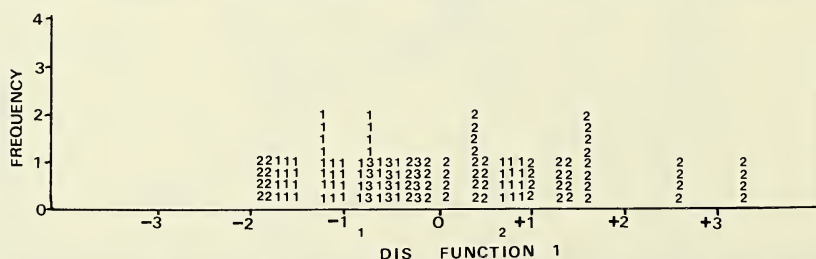


Fig. 4.—Frequency histogram of discriminant function 1 versus frequency. Each column of four figures represents a specimen. 1 denotes the yellow morph, 2 the black morph and 3 overlapping cases. Small 1 and 2 below baseline show group centroids.

Outjo districts (Lawrence 1928). Although the two scorpions are very similar morphologically, certain differences are apparent. The most obvious one lies in the length of the stridulatory patch on caudal segment 2. In *villosus* this shagreened area is oval and restricted to the anterior two thirds of the segment. In *brachystylus* it extends as a broad parallel-sided row of granules to the hind end of the segment. In addition to this, the first caudal segment is longer than wide in *villosus* and *vice versa* in *brachystylus* (Fig. 5). The width percentage of length was reported to be 92 - 98% in *villosus* and 103 - 109% in *brachystylus* (Lamoral 1979).

Differences in haemolymph phoreograms between *villosus* and *brachystylus* have been reported (Lamoral 1979). Electrophoresis of venom and haemolymph on Sodium Dodecyl Sulphate polyacrylamide gels, resolving up to 25 bands per sample, failed to reveal significant differences between *P. villosus* and *P. brachystylus* (Harington pers. obs.). Non denaturing disc electrophoresis of haemolymph did not show any differences either.

On reanalysis the "diagnostic" morphological features proved to be subject to extensive variation. This flux is concentrated in an area juxtaposed between the main distributions of the two scorpions. The nature of this variation is apparent in Fig. 5. Two ratios, w/l_1 (width/length of caudal segment 1) and s/l_2 (length of stridulatory area/length of caudal segment 2) were calculated to track the change in morphology. These parameters were then plotted against latitude (Figs. 6, 7). In addition, the discriminant scores of three classes, namely *villosus*, intermediates and *brachystylus*, were plotted against latitude (Fig. 8). The discriminant score gives a more inclusive assessment of morphological differences than simple ratios. The three most important characters used in the calculation of the discriminant scores were: length of caudal segment 3, length of stridulatory patch and length of caudal segment 1 (see Table 6). Clearly, neither the usual morphological features nor any one or more the 15 metrical characters can be considered as being truly diagnostic. These scorpions are not allopatric, but rather parapatric (narrowly sympatric). An analysis of the distribution of two parental forms and the intermediates allowed a intergradation zone be located roughly within a rectangle delimited by the Ugab river mouth site, Ugab drift about 32 km N of Uis, Uis, and a locality 43 km N of Cape Cross. At two localities, Uis and the Ugab mouth site, both parental types and the intermediates are sympatric. At Uis, *villosus*, intermediates and *brachystylus* composed 13, 60 and 27% of the population respectively ($n = 15$). It is of interest to note that this zone, at approximately 50 km broad, is slightly wider than the color intergradation zone of *P. villosus* (Fig. 9).

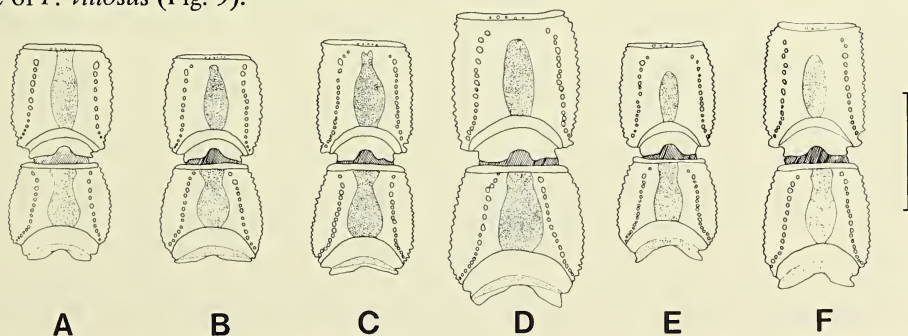
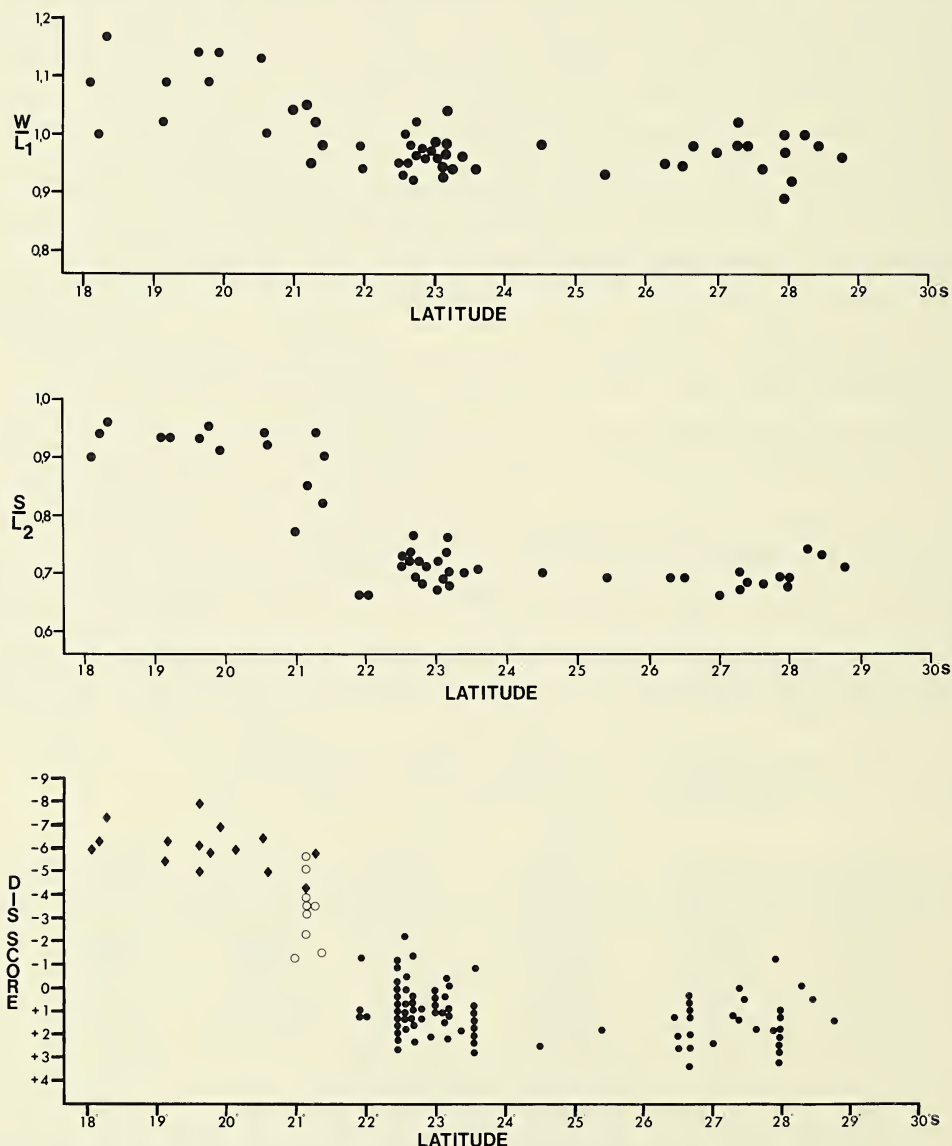


Fig. 5.—Dorsal view of caudal segments 1 and 2. A, Typical *P. brachystylus*; B and C, intermediates close to *brachystylus* (C has a tail shape more characteristic of *villosus*); D, intermediate; E, *P. villosus* with *brachystylus* - like first caudal segment; F, typical *P. villosus*. Setation has not been illustrated and the scale represents 1 cm.

Stepped clines as illustrated in Figs. 6, 7 and 8 are often characterized by increased variability within the intergradation zone. In order to assess this variation and to further analyse the importance of morphological differences between *villosus* and *brachystylus*, a multivariate analysis was done. Specimens were assigned to their particular group on the basis of the length of the stridulatory patch.

Results.—Table 2 gives the group means and standard deviations of variables measured. Table 3 gives standardised discriminant function coefficients. Fig. 10 is a scatterplot of discriminant scores against the two discriminant functions. Several interesting conclusions can be drawn from the results. The increased variability present within the intermediates



Figs. 6-8.—Fig. 6, the ratio w/l_1 plotted against latitude; 7, the ratio s/l_2 plotted against latitude; 8, discriminant score of *brachystylus* (diamonds), intermediates (circles), and *villosus* (dots), is plotted against latitude.

Table 2.—Group means and standard deviations for each morphometric measurement of *P. villosus*, *P. brachystylus* and intermediates in micrometer units (1 micrometer unit = 0.15 mm).

Variable	VILLOSUS		BRACHYSTYLUS		INTERMEDIATES	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Length cauda 1	53.78	5.56	44.00	8.84	51.73	8.95
Width cauda 1	51.58	5.27	47.33	8.24	53.72	9.13
Length cauda 2	60.67	5.79	50.37	9.44	58.45	9.67
Width cauda 2	50.00	4.88	46.20	7.50	52.36	8.66
Stridulatory length	42.94	4.83	46.83	8.77	48.95	7.84
Length cauda 3	61.16	5.88	51.90	9.50	59.68	9.71
Width cauda 3	48.83	4.64	45.27	7.28	51.32	8.68
Length cauda 4	66.23	6.38	56.30	10.58	65.66	10.65
Width cauda 4	47.37	4.68	44.03	7.28	49.64	8.14
Length cauda 5	69.21	7.02	57.87	10.35	67.18	10.63
Width cauda 5	40.34	4.05	38.17	6.27	42.73	7.63
Length telson	85.98	7.78	76.27	13.50	86.79	12.62
Width telson	43.88	6.73	39.60	8.37	45.86	8.74
Length patella 1	44.12	3.37	38.47	6.72	43.18	5.90
Length patella 4	72.73	5.68	62.60	10.45	71.36	9.74

in spite of their restricted geographical distribution is clearly apparent. The length of the stridulatory patch as an indicator of the intermediate class is slightly biased in that it chooses intermediates that are slightly closer to *brachystylus*. However, designation of intermediates by this means remains very efficient as a reclassification success of 97% (Table 4) was obtained.

DISCUSSION

Intergradation zones and their associated step clines can be produced in two ways. In the case of primary intergradation, the clines developed while the populations were in continuous contact (Mayr 1963:369). Natural selection played a direct role in the differentiation process. In the case of secondary intergradation, two populations now connected by a steeply sloping character gradient were completely separated at one time but have come into contact after differences had evolved (Mayr 1963:369). On interbreeding an intermediate zone is produced. Endler (1977) has shown mathematically that clines resulting from secondary contact will rapidly decay and become gradual if there are no factors to prevent this. By the same token, clines due to primary intergradation will disappear unless selective gradients across the intergradation zones exist. The next part of the paper discusses possible factors which could be in operation to maintain the intergradation zones between the color morphs and between *villosus* and *brachystylus*.

1. **Hybrid disadvantage.**—For the purpose of discussing this factor it is assumed that hybridization between the parental form is taking place. According to Barton (1979), the existence of disadvantaged heterozygotes is a simple and obvious explanation for the existence of a narrow hybrid zone. Such hybrids may be inferior in viability, fertility, fecundity or mating success (*vide supra*). While this may be a factor maintaining the step clines described, all living intermediates I have seen are very fit. This does not necessarily extend to their Darwinian fitness. The fact that a range of intermediates is encountered

in both zones suggests that further crossing is probable. A test of this would be to demonstrate that hybridization is occurring and that gravid hybrid females exist.

2. Adaptation of morphs to different physical environments.—Studies on skinks (Huey and Pianka 1977) and desert geckos (Huey 1979) have shown that adaptations to different physical environments may well account for some parapatric distributions. An analysis of the distribution patterns of color morphs, *brachystylus*, and intergradation zones, revealed a good correlation with the occurrence of vegetation types determined by Geiss (1971) (Fig. 3). Furthermore, the width of the step clines correlates with the abruptness of the vegetation changes. In broad terms, the black morph is found in the Central Namib and Semi-desert areas (2 and northern 4) with *brachystylus* in the Mopane Savannah (5) to the north of this. Towards the south, the yellow morph dominates, in the Savannah Transition (4), Highland Savannah (8) and Dwarf Shrub Savannah (9) vegetation zones. The southern black legged morph is virtually confined to the very arid Desert and Succulent Steppe (lower 3). It is interesting to note the absence of all these scorpions in the Kalahari Savannah (11, 12, 13) probably due to the absence of rock cover.

All three of the intergradation zones lie in areas where change in vegetation type is abrupt. Other less significant changes in vegetation type take place within the ranges of the scorpions.

(a) *villosus-brachystylus* intergradation zone: Change over in vegetation here occurs over about 50 km (E. R. Robinson, pers. comm.) which corresponds to the intergradation zone. A drop in altitude occurs simultaneously.

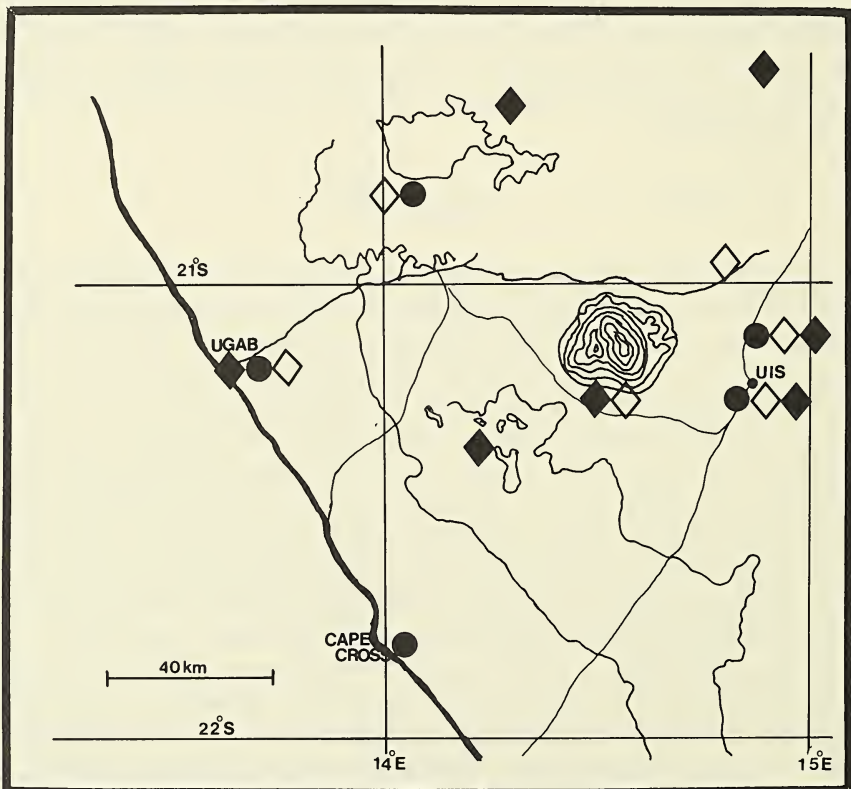


Fig. 9.—Map showing location of the *villosus-brachystylus* intermediate zone. Black diamonds represent *brachystylus*, open diamonds and dots denoting intermediates and *villosus* respectively.

Table 3.—Standardised discriminant function coefficients for each variable used in discrimination procedure of *villosus* - *brachystylus* analysis. Best discriminating variables are indicated by asterisks.

Variable	Function 1	Function 2
Length cauda 1	2.079*	-0.010
Width cauda 1	-1.719	-1.070
Length cauda 2	1.754	-1.676*
Width cauda 2	1.531	3.452*
Stridulatory length	-2.381*	-0.287
Length cauda 3	-2.503*	-1.311
Length cauda 4	1.476	2.996*
Width Cauda 4	-1.081	-1.050
Length cauda 5	0.606	-1.260
Width cauda 5	-0.640	-0.145
Length patella 4	0.808	1.018

(b) Central zone: An estimate for the vegetation transition zone is 10 -20 km (E. R. Robinson, pers. comm.) which corresponds to the observed color intergradation zone. The presence of the savannah-associated yellow morph within the Central Namib may be associated with mountains and riverbeds where less xeric habitats and vegetation are found. The yellow morph is mainly found in association with the Kuiseb river and the Arachdamb - Tumas mountain area.

(c) Southwestern zone: The transition in vegetation between Dwarf Shrub Savannah (9) and Desert and Succulent Steppe (lower 3) is very sharp and changes over a distance of about 10 km (E. R. Robinson, pers. comm.). Towards the southern area of this zone where intermediates are known, the transition in vegetation is less abrupt due to presence of mountains and rivers (E. R. Robinson, pers. comm.). Although the farm Tsirub 13 falls within Succulent Steppe (lower 3) observations in the field clearly show that it is a marginal locality in terms of vegetation. No southern black morphs have been taken 40 km eastwards on the more vegetated farms Aar 16 and Plateau 38 where the yellow morph is common.

3. Low vagility.—It has been shown (Endler 1977) that the width of a cline is affected by the amount of gene flow between the interacting taxa. If gene flow is minimized a cline can remain differentiated for long periods. According to Endler, gene flow is generally increased by large numbers of individuals moving long distances. Alternatively, if gene flow takes place over short distances differentiation may be very high. Scorpions are

Table 4.—Classification results of *P. villosus* - *brachystylus* analysis. Percent of grouped cases correctly classified 97.3%.

Actual group	No. of cases	Predicted 1	group 2	membership 3
1. <i>villosus</i>	123	121 98.4%	0 0.0%	2 1.6%
2. <i>brachystylus</i>	15	0 0.0%	14 93.3%	1 6.7%
3. intermediates	12	0 0.0%	1 8.3%	11 91.7%

not particularly mobile and this low vagility may well be an important factor involved in the maintenance of the step clines.

In conclusion, hybrid inviability, adaptations to different physical environments and low vagility may all be involved to a lesser or greater degree in the maintenance of the parapatric distribution described.

CONCLUSION

Whether primary or secondary intergradation is involved, there is little doubt that the various color morphs and *P. brachystylus* are members of the same species. If natural selection played a direct role in the creation of the cline (primary intergradation) sympatric speciation would have to take place. This is highly unlikely (Futuyma and Mayer 1980). If the clines are caused by hybridization after change in allopatry (secondary intergradation) speciation should largely be complete or occur by parapatric interaction. The frequency of intermediates (which would be hybrids if secondary intergradation is implicated) is sufficiently high to suggest that the parentals would be recognizing each other efficiently. This is indicative of conspecificity (Paterson 1980). Lastly, parapatric speciation is not probable (see Futuyma and Mayer 1980).

P. brachystylus is thus regarded as a subspecies of *P. villosus*. This is partly an arbitrary decision since the color morphs have integration zones as steep as that in the *P. villosus-brachystylus* case. The degree of morphological divergence over such a zone is not relevant to determining whether the "pure" forms on either side of the zone are good species.

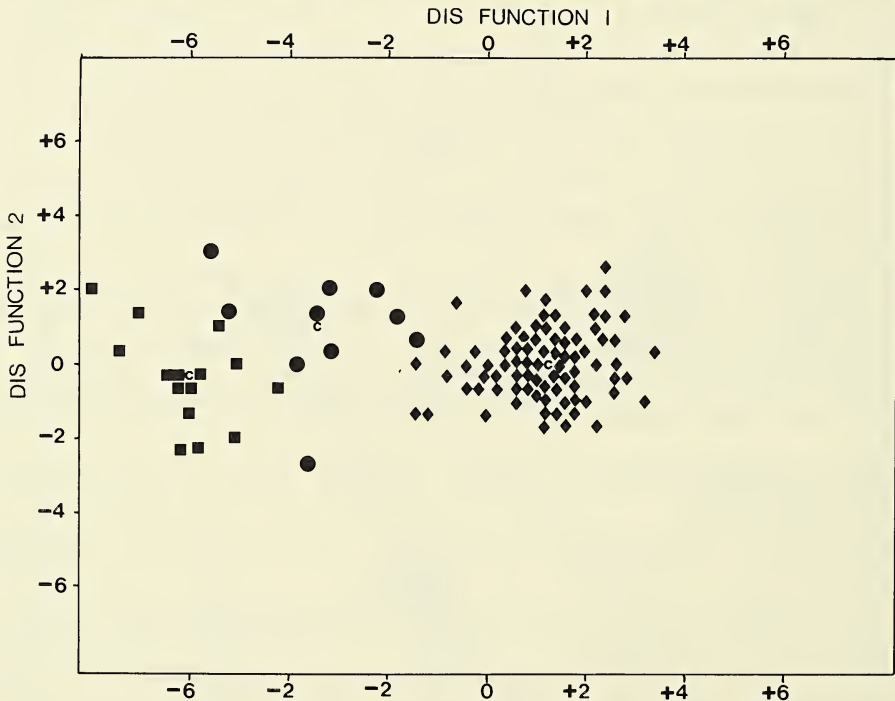


Fig. 10.—Scatterplot of the discriminant scores of discriminant functions 1 and 2 plotted against each other. Squares, dots and diamonds denote *brachystylus*, intermediates and *villosus* respectively. Group centroids are indicated by c. Note that some intermediates share certain discriminant scores with the parental groups.

Morphology has a strictly secondary role as a criterion of species rank (Mayr 1963, Short 1969).

TAXONOMIC CHARACTERIZATIONS

Parabuthus villosus (Peters) 1862.

Buthus villosus Peters 1862:26.

Within the genus *Parabuthus*, *P. villosus* can be diagnosed as follows.

Diagnosis.—Caudal segment 4 with 10 strong granular keels. Ventral keels indistinct posteriorly on this segment. Tail narrowing posteriorly, caudal segment 4 narrower than 1 (rarely equal in width). Dorsal view of dorso-lateral keels subparallel. Stridulatory area on caudal segment 1 broad, composed of strong granules, occasionally forming short ridges. Color of trunk blackish brown to black. Cauda usually pilose.

Parabuthus villosus villosus (Peters)

Diagnosis.—Dorsal stridulatory area on caudal segment 2 confined to a narrow oval and usually depressed area. Does not approach posterior margin of segment appreciably, $s/1_2$ ratio between 0.63 and 0.82 (mean = 0.71). Width of caudal segment 1 usually less than length, $w/1_1$ ratio from 0.88 to 1.08 (mean = 0.97). Distributed south of $21^{\circ}10'S$, Namibia.

Parabuthus villosus brachystylus, new combination

P. brachystylus Lawrence 1928:270-73.

Diagnosis.—Dorsal stridulatory area on caudal segment 2 present as fairly narrow channel, reaching posterior margin of segment. $s/1_2$ ratio between 0.90 and 0.96 (mean = 0.93). Width of caudal segment 1 generally greater than length, $w/1_1$ ratio between 0.96 and 1.17 (mean = 1.08). Found north of $21^{\circ}10'S$, Namibia.

P. v. villosus — *P. v. brachystylus* intermediates

Dorsal stridulatory area approaching posterior margin of segment, $s/1_2$ ratio between 0.77 and 0.90 (mean = 0.85). $w/1_1$ ratio between 0.98 and 1.11 (mean = 1.05). Distributed in a narrow zone between $21^{\circ}10' - 21^{\circ}20'S$, Namibia.

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AGONISTIC BEHAVIOR IN FEMALE WOLF SPIDERS (ARANEAE, LYCOSIDAE)

Mary E. Nossek and Jerome S. Rovner

Department of Zoology
Ohio University
Athens, Ohio 45701

ABSTRACT

We observed the sequences of behaviors shown during encounters between individuals in conspecifically and heterospecifically grouped adult female *Lycosa punctulata*, *L. rabida*, and *L. helluo*. Significant linkages within pairs of successive acts between individuals were revealed, indicating that some behaviors have communicatory effects. There were no major differences among the three species in the forms of behaviors shown, nor in the sequences of these behaviors, the sequences being highly variable. Some of the behaviors, and perhaps their sequence variability, probably inhibit approach and/or attack, thus resulting in spacing of the individuals. Cannibalism was infrequent (< 1%) within conspecific as well as heterospecific groups. Food deprivation did not increase cannibalism within conspecific groups of post-mating age females, suggesting either that hunger does not increase the level of aggressivity among conspecific females of this physiological class, or that hunger lowers their fighting potential and thereby increases their avoidance tendency.

INTRODUCTION

Aggression, defined as "overt behavior directed at harming or threatening to harm another individual with the intent of gaining some advantage" (Wittenberger 1981), is well-known in spiders. Since aggressive behavior involves risks, even to the attacker, withdrawal components occur in both individuals during interactions; consequently, the term "agonistic behavior," which includes withdrawal as well as threat and attack, is applied to the set of behaviors occurring in aggressive interactions (ibid.).

Various observers have noted intraspecific fighting between male spiders (e.g., Montgomery 1910, Bristowe 1929, Kaston 1936, Rovner 1968a, Robinson and Robinson 1980). A number of workers have described leg-waving displays during male-male encounters in wandering spiders (e.g., Crane 1949, Rovner 1968b, Dijkstra 1970, Aspey 1977a). Two studies detailed agonistic behavior in female web-weaving spiders (Buskirk 1975, Riechert 1978), in which vibrational cues provided important signals. As Riechert (1982) emphasized, spiders can recognize conspecifics as competitors, as opposed to potential prey or predators, and typically use communication rather than fighting in encounters with conspecifics.

When killing of a conspecific does occur in spiders, it usually is followed by ingestion, i.e., by cannibalism. Whether the killing of a conspecific by a spider results from an aggressive tendency or a predatory one is not readily determined. Since wolf spiders

scavenge dead arthropods (Knost and Rovner 1975), the cannibalism that follows a killing may represent a response to a feeding tendency that itself did not trigger what was primarily an aggressively motivated attack. Aggressive attacks have been reported in lycosids by Schaefer (1972), who described cases of interspecific killing of competitors in which the rival was not subsequently eaten. On the other hand, it is possible that hunger is the prime motivation for what is, in some cases, a predatory attack. If the latter is sometimes so, one expects to find higher levels of killing and cannibalism in food-deprived than in sated spiders.

In wolf spiders, cannibalism regularly occurs among juveniles (e.g., Hallander 1970); leg-waving behavior is thought to reduce the level of killing among them (Koomans et al. 1974, Aspey 1975). In the laboratory, adult female lycosids sometimes cannibalize adult male or female conspecifics, whereas adult males observed under similar conditions do not (e.g., Rovner 1968b, Hallander 1970). Visual and acoustic threat displays have been described that are used during male-male agonistic interactions (e.g., Vlijm and Dijkstra 1966, Hallander 1967, Rovner 1968b, Dijkstra 1970, Aspey 1976, 1977a, b). Prior to the present study, such displays had not been described for female-female encounters in wolf spiders.

Rovner (unpubl. data) observed that leg-raise behavior and dominance relationships, rather than cannibalism, occurred in a group of adult female *Lycosa helluo* Walckenaer housed in a terrarium. Likewise, Nossek (unpubl. data) noted leg raises and waves in adult female *Schizocosa ocreata* (Hentz) and *S. saltatrix* (Hentz) when conspecific groups of each species were housed in terraria. Cannibalism occurred in only 3% of their interactions. With these preliminary data in mind, we decided to focus on agonistic behavior in female wolf spiders as the subject for the present study. We sought: (1) to provide the first descriptions of agonistic behavior in female lycosids; (2) to determine if behaviors occur that may inhibit intraspecific approaches and/or attacks; (3) to determine if such behaviors are generalized enough to inhibit heterospecific approaches and/or attacks; and (4) to examine the effect of presumed increased hunger levels on the incidence of killing and cannibalism.

GENERAL METHODS

Experimental Design.—Intraspecific encounters were observed in *Lycosa punctulata* Hentz, *L. rabida* Walckenaer, and *L. helluo* Walckenaer during September through December, 1979. For each of two species, *L. punctulata* and *L. rabida*, six groups with five adult females per group were maintained for 30 days; four such groups were used for *L. helluo*. Spiders were grouped according to size, based on carapace width (within 0.5 mm). Half of the groups of each species were fed daily, whereas the others were not fed during the 30 days. (The methods for observing interspecific encounters are described later.)

Subjects.—Spiders were collected from fields near Amesville, Athens County, Ohio, U.S.A. Most *L. helluo* were collected as adults (September), all *L. punctulata* as adults (September), and most *L. rabida* as penultimate instars (early July). (Although the mating history of the adults was unknown, none of the spiders used in the group experiments produced offspring.) Spiders were kept isolated from each other until the onset of the experiment. Each was offered a larval *Tenebrio molitor* every 2-3 days prior to being grouped. Before grouping, each spider was anesthetized and measured (width at widest

point of carapace) and then dabbed with a spot of non-toxic enamel ("Pactra-namel," Los Angeles) on the carapace and/or abdomen.

Observation Chambers.—In studies involving conspecifics, groups of spiders were housed in glass-covered, glass-walled terraria measuring 50 X 25 X 30 cm high; consequently, density was established as one spider per 250 cm² of floor space. The floor was covered with cm² graph paper to aid in noting interindividual distances maintained within each group. The paper formed a 3-cm lip around the sides that eliminated visual contact between groups and prevented reflection of a spider from the wall. Distilled water was provided by four cotton-stoppered vials, each in one quadrant of the tank. Also, a water-filled watch glass (5-cm diameter) was in the center to provide relatively high humidity. Photoperiod and temperature were not controlled.

Data collection.—Following the initial placement of spiders in a tank, observations were made for 1 hr, during which all spider activities were recorded. Distances between spiders were noted at the end of every 5-minute period. Each group was observed subsequently for 20 min per day for 30 days. Interspecific groups were observed initially for 1 hr and subsequently for 30 min per day for 10 days. Observation times for all groups were varied throughout the day (0800-2000 hr).

The following were noted for all interactions: initiating spider; responding spider; distance between them when the first behavior occurred; and the frequency and sequence of behaviors as they occurred. The observer's face was about 20-30 cm from the front of the terrarium. Protocol was whispered into a hand-held microphone, the tape recorder being located on a separate table from that supporting the terraria.

DESCRIPTIONS OF BEHAVIORS

Based on preliminary observations of paired spiders (not used in later group experiments) and aided by photographs and movies of grouped spider interactions, we developed the following list of behaviors associated with encounters of female *Lycosa* spp. These occurred in all three species, except for Acute Flex and Jerky Wave (*L. rabida* and *punctulata* only) and Prolonged Touch (*L. rabida* only). Based on Aspey's (1977a) evidence for a signaling role for similar postures and movements in male *S. ocreata*, it is probable that some of the behaviors occurring in these female *Lycosa* spp. likewise provide information to conspecifics, certain of them perhaps having evolved largely for communication.

Locomotory Behaviors

Approach Behaviors

1. Close Approach—movement of one spider to within 6 cm of another. It usually results in a response from one or both individuals.

2. Follow—to walk or run after a retreating spider for a minimum distance of 3 cm. It sometimes involves an exaggerated walk, with a high stepping motion of Legs I. Follow becomes Close Approach (and the start of a new interaction) when the distance between two individuals is 6 cm or less.

3. Step-Wave—hyperextension of one or typically both legs I during forward motion, usually after a brief interaction with another individual. At the top of the raise, the femora are held at an angle of 40-60° relative to the substrate. Slow forward motion continues as the forelegs are lowered simultaneously to the substrate and once again hyperextended and raised.

4. Lunge—a forward and upward thrust of the body in the direction of the other spider, with the chelicerae widespread. It occurs only when the spiders are within 3 cm of one another, but does not always result in contact.

Avoidance Behaviors

1. Retreat—one spider turns and walks or runs away from the other. Sometimes one spider runs directly over the top of the other and beyond. Retreat terminates an interaction unless Follow occurs.

2. Mutual Avoid—simultaneous retreat of two interacting individuals.

3. Jump—the spider kicks out with one or more legs and leaves the substrate in a short upward or backward hop. It then flattens its body against the substrate with the legs outstretched or Retreats.

Leg Raises

These involve a single leg or adjacent pairs of legs. If face to face, the spider raises both legs I; sometimes legs II are also lifted. If approached diagonally, the spider raises one corresponding leg I and often the adjacent leg II. Approached posteriorly, the spider either turns around and raises its forelegs or keeps its orientation and raises leg III and/or leg IV. The lifted legs are held up for a variable length of time, depending on the behavior of the other spider. If the opponent remains immobile or Retreats, the first spider may hold the raised leg posture for as long as 3 min.

Leg Extensions (listed in order of increasing leg elevation)

1. Horizontal Extend of any leg (Aspey 1977a)—the extended (straight) leg is raised and held roughly parallel to the substrate (see spider on right in Fig. 1).

2. Oblique Extend of any leg (Aspey 1977a)—the femur of the extended (straight) leg is raised to, and held at, an angle of $45\text{--}60^\circ$ relative to the substrate.

3. Vertical Extend of legs I (Aspey 1977a)—the femora of the extended (straight) legs I are raised to, and held at, an angle of $60\text{--}90^\circ$ relative to the substrate, and the abdomen is lowered as the body tilts posteriorly. Legs II often are concurrently raised and held in an Acute Flex (see below).

Leg I Flexions (listed in order of increasing leg elevation)

1. Acute Flex—the leg I femora are raised and held at a $30\text{--}60^\circ$ angle relative to the substrate, and the femoro-patellar and tibio-metatarsal joints are flexed.

2. Vertical Flex—the leg I femora are raised and held at a $60\text{--}90^\circ$ angle relative to the substrate, and the femoro-patellar joints are flexed (see spider on right in Fig. 2).

3. Obtuse Flex—a strong flexion of the trochantero-femoral joint of legs I, resulting in the femora pointing posteriorly $95\text{--}140^\circ$. The patella and tibia are pointed obliquely 50° ; and the metatarsus and tarsus are held almost parallel to the femur (see spider on left in Fig. 1). Legs II and III are directed anteriorly and touch the substrate. The chelicerae are slightly spread.

4. Obtuse Flex-Body Raise—in addition to an Obtuse Flex posture of legs I, the cephalothorax is raised (and the abdomen pointed down), so that the longitudinal axis of the body is at least 30° relative to the substrate (Fig. 3). Legs II are raised, held in an Obtuse Flex, and spread laterally. The chelicerae are spread widely. Often the palps are folded and tucked against the chelicerae.

Contact Behaviors

1. Touch—occurs when one spider's foreleg(s) contacts the legs or body of the other. This usually results in Retreat; however, sometimes there is either no response or the leg contacted is raised into a leg extension. Grapple occasionally follows Touch.

2. Prolonged Touch (only seen in *L. rabida*)—occurs when there is no response from the contacted animal, and the spider initiating the contact remains touching the other for a period greater than 3 sec. This can last up to 20 min.

3. Grapple—results from a Lunge by one or simultaneous Lunge by both spiders, and involves ventral-ventral orientation maintained by mutual grasping (Fig. 4). The chelicerae are spread and sometimes locked together. However, if anterior-anterior orientation is not also involved, due to a slow response by an attacked spider or if attack from the posterior occurred, a fatal bite on the cephalothorax or anterior abdomen sometimes occurs. Usually, Grapple results in separation and a running Retreat by one or both spiders. Grapple durations ranged from 5 to 132 sec, averaging 56 sec.

Other Behaviors

1. Resting—body parallel to the substrate and either raised, with legs extended and tarsi flat on the substrate, or contacting the substrate, with all legs extended or else flexed



Fig. 1.—Agonistic interaction between adult female *Lycosa punctulata*. The one on the left is performing Obtuse Flex, whereas that on the right shows Horizontal Extend.

Fig. 2.—Vertical Flex in an adult female *L. punctulata* (facing the camera).

at the tibio-metatarsal joint and held close to the body (only the tarsal tips touching the substrate).

2. Hyperactivity—random running, contact with other spiders, and subsequent mutual avoidance. It occurs at least once in the first hour after introduction to the tank and usually involves all the spiders.

3. Jerky-Wave (*L. punctulata* and *L. rabida*)—forelegs oriented toward a retreating spider and raised simultaneously, then lowered jerkily. It usually occurs after a brief



Fig. 3.—Obtuse Flex-Body Raise in two adult female *L. punctulata*.

Fig. 4.—Grapple in adult female *L. punctulata*.

encounter but resembles the leg-waving display performed by female *L. rabida* during courtship (Rovner 1968b).

4. Palpal Drumming—palps alternately lifted and lowered in rapid succession, usually but not always contacting the substrate. It occurs rarely and is seen in situations when one spider follows another and then halts.

Construction Activities

1. Nest Construction—occurred in 10 of the 16 tanks and resulted in silken cells made in the entrance of water vials or in the corners of tanks. Nests were often built just prior to egg sac construction but were not a prerequisite for the latter. Furthermore, nests were built and used without subsequent egg sac construction. Nest use was not limited to the individual that originally had built a particular nest.

2. Egg Sac Construction—occurred in the following: 4 of 30 *L. punctulata*, 3 of 20 *L. helluo*, and none of 30 *L. rabida*. All the egg sacs were subsequently destroyed and discarded by their owners, which indicated that viable eggs were not present (Eason 1969, Rovner unpubl. data). Spiders carrying egg sacs were reclusive and rarely emerged from water vials or silk nests; thus, possible differences in responsiveness to the approach of other spiders could not be studied.

INTRASPECIFIC AGONISTIC INTERACTIONS

Methods.—We wished to control density so as to minimize effects of the restricted lab conditions and yet allow for “normal” interactions. Aspey (1977a) manipulated densities of grouped male *S. ocreata* and found a significant effect of spatial density on the number and types of interactions: the greatest number of displays occurred between spiders in less crowded tanks. We provided 250 cm² unit floor space per individual, which exceeded the relative maximum space per individual used by Aspey.

An interaction was considered to occur when one spider approached the other to within 6 cm, the distance at which an approach usually elicited a response. Distances were measured along the substrate grid from the palp of one spider to the closest palp of the other (Aspey 1977a). The sequence of acts of the two individuals was recorded without regard to durations. All pairs of successive acts then were entered in a matrix of interindividual 2-act sequences, with initial acts in horizontal rows and following acts in the vertical columns. Table 1 summarizes the numbers of interactions observed.

To determine whether a behavior by one spider was linked significantly to that of the other, chi-square tests were used. Data for the three species were combined to test for linkages within pairs of successive acts, thus providing 491 interactions for a total of 1250

Table 1.—Summary of the interactions observed in conspecific groups of adult female spiders of the genus *Lycosa*.

Species	Hours obs.	No. observed interactions	No. observed behaviors	Mean no. behaviors per interaction	Range of no. behaviors per interaction
<i>L. punctulata</i>	64	167	452	2.71	1-7
<i>L. rabida</i>	64	212	468	2.21	1-5
<i>L. helluo</i>	43	112	330	2.95	1-6
Total	171	491	1250		

behavioral acts. The transition matrix of Table 2 consequently represents the frequencies of each behavior's occurrence in relationship to the occurrence of another behavior for the three species of *Lycosa* combined.

Table 2.—Transitional probabilities of interindividual behavior sequences during interactions of adult female *Lycosa* spp. The underlined transitions departed significantly (chi-square, $P < 0.05$) from the expected probabilities. Abbreviations: CA = Close Approach; FO = Follow; MA = Mutual Avoid; RT = Retreat; JU = Jump; HE = Horizontal Extend; OE = Oblique Extend; VE = Vertical Extend; AF = Acute Flex; VF = Vertical Flex; OF = Obtuse Flex; OF-BR = Obtuse Flex-Body Raise; LU = Lunge; TO = Touch; PTO = Prolonged Touch; GR = Grapple.

	CA	FO	MA	RT	JU	HE	OE	VE	AF	VF	OF	OF-BR	LU	TO	PTO	GR	
CA	6	0	6	<u>141</u> ⁽⁻⁾	18	<u>24</u>	<u>106</u>	37	9	<u>32</u>	<u>26</u>	14	36	40	0	0	495
FO	0	<u>19</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
MA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RT	0	<u>65</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65
JU	0	0	0	<u>33</u>	0	0	0	1	0	0	0	1	3	5	0	0	43
HE	0	0	<u>3</u>	9	0	0	7	3	0	0	0	2	<u>7</u>	<u>10</u>	0	0	41
OE	0	0	4	67	0	8	15	<u>20</u>	0	8	10	3	12	10	0	0	157
VE	0	0	0	<u>43</u>	0	<u>6</u>	9	0	0	3	0	0	9	3	0	0	73
AF	0	0	0	2	0	0	0	<u>2</u>	0	1	<u>2</u>	0	0	0	0	0	7
VF	0	0	0	15	<u>7</u>	1	10	5	0	0	4	3	3	0	0	0	48
OF	<u>1</u>	0	0	10	0	1	<u>14</u>	1	0	0	0	1	1	0	0	0	29
OF-BR	0	0	0	8	0	0	3	0	0	0	0	0	<u>10</u>	0	0	2	23
LU	0	0	0	<u>64</u>	7	0	0	5	0	0	0	0	0	11	0	<u>31</u>	118
TO	0	0	5	41	<u>11</u>	0	<u>4</u> ⁽⁻⁾	0	0	<u>9</u>	0	<u>7</u>	<u>17</u>	0	<u>12</u>	0	106
PTO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR	0	0	<u>10</u>	<u>16</u>	0	0	0	0	0	0	0	0	0	0	0	0	26
	7	84	28	449	43	38	168	74	9	53	44	31	98	79	12	33	1250

Results.—Table 2 shows that the occurrence of some behaviors deviated significantly from expected probabilities. Of 256 possible linkages in the 16 X 16 matrix, 28 occurred more frequently than expected by chance; and 2 were negatively linked, occurring less frequently than expected. Behaviors with significant linkages are represented in Fig. 5, which only includes those leg postures that also were significantly linked at the species level in all three species.

A wide variety of behaviors followed Close Approach or Touch, but very few consistently followed any of the other preceding behaviors. For example, Oblique Extend was followed only by Vertical Extend, while Vertical Extend was followed only by Horizontal Extend or Retreat. Vertical Flex was followed only by Jump; while Jump was followed only by Retreat. Obtuse Flex-Body Raise probably indicated a greater likelihood of defensive attack than the other leg flexions or extensions, as it typically occurred only when the other spider continued to approach after an initial signal was given and was accompanied by widely spread chelicerae.

Step-Wave and Jerky-Wave, infrequently occurring behaviors, were not included in the transition matrix because both behaviors, when they did occur, appeared as a delayed response to the Retreat of another spider. The only context in which they appeared was following brief encounters between recently grouped spiders. Typically, one spider walked within 6 cm of another and quickly Retreated in response to the turning or orienting movement of the Approached spider. Step-Wave or Jerky-Wave might then be performed by the Approached spider 3-5 sec later, in the direction of the Retreating spider.

Following an encounter, a spider often flattened itself, with its body on the substrate and its legs outstretched. This lasted up to several min.

Of 491 observed encounters between conspecifics, only 4 (0.8%) resulted in cannibalism. Most encounters did not go beyond display to fighting. Leg raises alone were usually sufficient for eliciting Retreat.

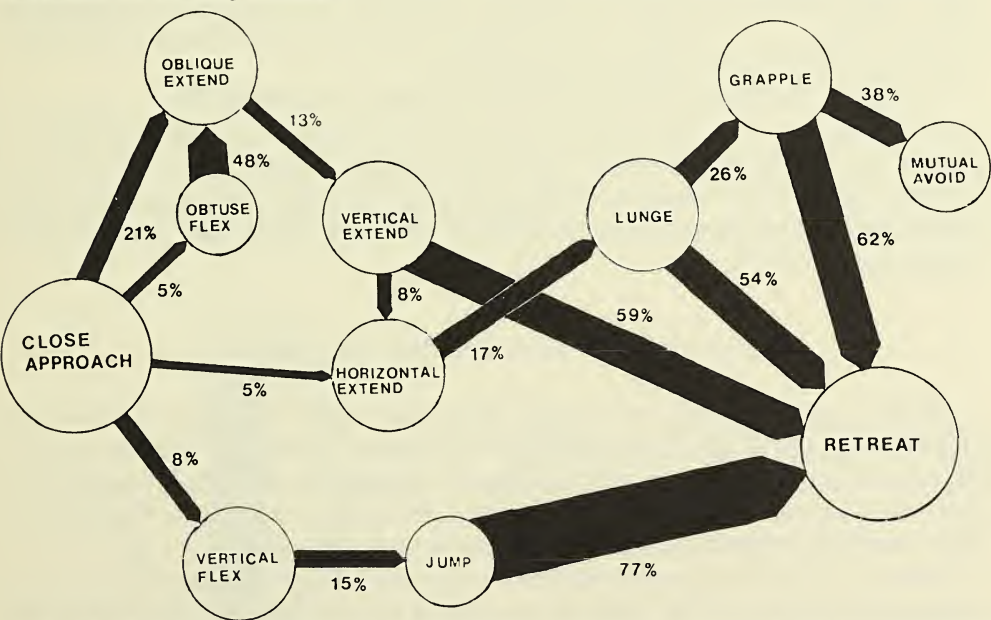


Fig. 5.—Transitional probabilities of interindividual behavior sequences during 491 conspecific interactions involving adult female *Lycosa* spp. Only significant linkages (chi-square, $P < 0.05$) are indicated, with the percentage of occurrence following a given behavior.

During this study, individual *L. punctulata* maintained an average distance from a nearest neighbor of 20 cm. Interindividual distances averaged 14 cm in *L. helluo* and 6 cm in *L. rabida*.

INTERSPECIFIC AGONISTIC INTERACTIONS

Introduction.—Hazlett (1974) analyzed aggressive displays used in heterospecific encounters between hermit crabs and found that the same display components elicited a response in more than one species. The interspecific signals were similar to intraspecific signals. Since relatively high levels of interspecific predation occur in some species of lycosids sharing the same habitat (Schaefer 1972), we anticipated that some of the behaviors observed in intraspecific encounters in our species of wolf spiders would also serve to inhibit approach or attack by heterospecifics.

Methods.—In January 1980, we established four observation chambers, each containing spiders of two different species. Two tanks each held two *L. rabida* and two *L. punctulata*. The other two tanks each contained two *L. rabida* and two *L. helluo*. The spiders were grouped according to similar carapace width and were offered insect prey daily during the 10-day study. Each spider had about 200 cm² of floor space.

Results.—Among the pairs of *L. punctulata* and *L. rabida*, interspecific predation only occurred once, when a *L. rabida* approached posteriorly and touched a *L. punctulata*. The *L. punctulata* turned quickly, and a Grapple resulted. The spiders separated after about 10 sec, but the *L. punctulata* ran after the Retreating *L. rabida* and pounced on it from behind.

Among the pairs of *L. helluo* and *L. rabida*, one *L. rabida* in each of the tanks was killed and fed upon in a heterospecific interaction. These kills occurred in the first encounter following introduction to the tank. In one instance the capture occurred when the *L. helluo* rapidly approached a walking *L. rabida* from the side and then pounced on it. In the other case, a *L. rabida* was climbing in a corner and was approached posteriorly. As it turned, the *L. helluo* lunged and captured it.

During the 10 days, none of the *L. helluo* nor the *L. punctulata* were captured. Encounters among the surviving spiders in all tanks were typified by Vertical Extend or Oblique Extend and Mutual Avoid. A generalized sequence, based on the 22 encounters observed during the 10 days, is shown in Fig. 6. The spiders maintained an average distance from their nearest conspecific neighbor of 9 cm and from their nearest interspecific neighbor of 15 cm.

BEHAVIOR DURING CAPTURE OF INSECTS

Methods.—Four hundred prey capture bouts were observed in grouped and isolated individuals of *Lycosa* spp. to determine if the behaviors occurring in predation on insects include some of the same ones used in orientation to and response toward conspecific and heterospecific female lycosids. The prey item (larval *Tenebrio* or juvenile *Periplaneta* up to the size of the spider) was placed about 4 cm in front of the spider.

Results.—A preferred range of prey size was identified, for each species of lycosid, that approximated 1/3 to 1/2 the spider's body size. In 187 cases of capture of preferred-size cockroaches, orientation toward the walking prey also included the adoption of the

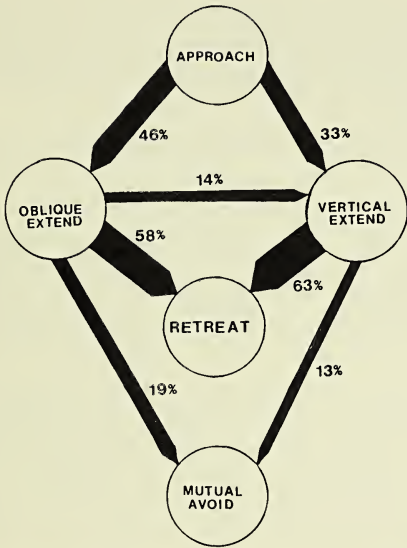


Fig. 6.—Transitional probabilities of interindividual behavior sequences during 22 heterospecific interactions between adult female *Lycosa* spp. Only significant linkages (chi-square, $P < 0.05$) are indicated, with the percentage of occurrence following a given behavior.

Acute Flex or Vertical Flex posture. The spider held the leg position as it slowly approached the prey or was approached by the prey. To the slow movement of *Tenebrio* larvae, the spider usually approached with a low Horizontal Extend.

Lunge and Pounce were sometimes preceded by a slight elevation of the cephalothorax, with chelicerae spread and forelegs raised. This posture differed from Obtuse Flex-Body Raise, which occurs in female-female encounters, where the body raise becomes progressively more pronounced if Retreat of the opponent does not occur. Also, the palps were rarely tucked prior to the Pounce of prey capture, but were held away from the chelicerae. Fig. 7 provides a generalized sequence of behaviors during capture of insect prey.

AGGRESSION IN HUNGRY VERSUS SATATED SPIDERS

Introduction.—The occurrence of cannibalism in some animals may represent a predatory response to a high level of hunger, but the effect of hunger is unpredictable based on studies to date. Fox (1975) cited several studies in which cannibalism in various taxa of

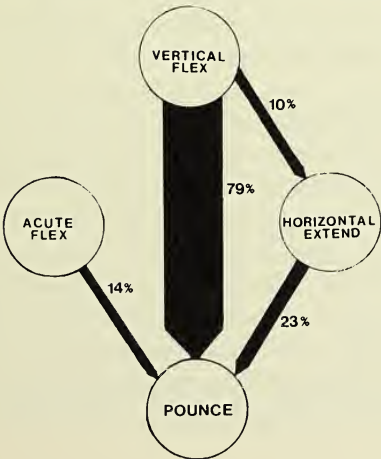


Fig. 7.—Transitional probabilities of behavior sequences in adult female *Lycosa* spp. during 400 captures of preferred-size prey. Only significant linkages (chi-square, $P < 0.05$) are indicated, with the percentage of occurrence following a given behavior.

animals was inversely related to the density of heterospecific food items. Although starvation increased the tendency to cannibalize in some animals, others responded merely to a decrease in the relative availability of heterospecific prey. Thus, high levels of hunger were not necessary to trigger cannibalism.

In regard to spiders, Jackson (1980) found a low level of cannibalism in the salticid *Phidippus johnsoni*; it increased only slightly after about 1 month of starvation in the post-reproductive females used in that experiment. Based on similar experiments with agelenids, Riechert (1982) also views adult spiders as not being highly cannibalistic. Krafft (1975) reviewed the behavioral mechanisms that inhibit intraspecific predation in spiders. Nonetheless, it is certain that some killing and cannibalism do occur in adult spiders; consequently, we wished to examine the effect of food deprivation on the level of cannibalism in adult lycosid spiders.

Methods.—Each species was grouped according to the experimental design described in the General Methods. Half of the groups of each species were offered prey daily and half not fed during the 30-day period, thereby operationally defining two hunger levels: well-fed and underfed. Not all well-fed spiders accepted prey (larval *Tenebrio* or juvenile *Periplaneta*) every time it was offered, but all did eat at least once a week (mean interval = 3 days). All surviving underfed spiders consumed prey on the day after the end of the experimental period, indicating that they were hungry and capable of prey capture.

We examined each tank once in the morning (0800-1000 hr) and once in the afternoon (1600-1800 hr). In addition to mortal combat directly observed, cannibalism was considered to have occurred whenever a spider was found dead within a tank. Whether the spider had been or was being fed upon was noted. A spider feeding upon an apparently freshly killed victim was assumed to be the cannibal. Dead spiders were removed as soon as possible without disturbing the surviving spiders. This meant that a cannibal in an underfed tank would no longer be under the influence of the same hunger level as the other spiders in the tank; but this was considered preferable to disturbing the spiders and thereby altering aggressive levels in the group. In all cases, the cannibalized spider was only partially consumed before its removal.

To test whether the frequency of cannibalism was associated with hunger level, a 2 X 2 test of independence using the G-statistic and Yates' Correction for small sample sizes was performed on the results for each species and for the results of the three species combined (Table 3) (Sokal and Rohlf 1969). Alive and Dead were the column variables; and hunger level (Well-fed and Underfed) provided the row variables.

Results for *Lycosa punctulata*.—Six kills occurred among well-fed spiders on the following days: day 1 (two kills), and days 8, 9, 20, and 25. Four kills occurred among underfed spiders (days 1, 5, 12, and 22). There was no association between hunger level and cannibalism.

In one group of well-fed spiders a single spider killed two others within a short time, events occurring as follows: During a Grapple, one spider killed a second and began feeding on it. A third spider joined in, resulting in mutual feeding, which lasted for about 90 sec. The result was a ball of spiders in which the legs of the feeding spiders interlocked, with the carcass between the occasionally tugging feeders. Then the two spiders released the carcass and Grappled for 50 sec. The spider that had made the original kill was again the winner. It dragged its second opponent to the first carcass (about a 10-cm distance), placed the body on top of the first one, and began feeding with its legs wrapped around both bodies. A fourth spider passed nearby, and the feeding spider responded with a Vertical Flex, using ipsilateral legs I and II. The fourth spider Retreated

but returned 9 min later and stopped 3 cm from the feeding spider. The latter Lunged, the pair Grappled briefly, and the fourth spider Retreated. The first spider performed leg I Jerky-Wave for 20 sec and then resumed feeding.

We directly observed only one other case of cannibalism, this among the underfed spiders. Signals were exchanged in the following sequence (each spider identified by subscript):

Approach₁—Vertical Flex₂—Vertical Extend₁—Lunge₂—Grapple

Grapple duration was approximately 160 sec and ended with the immobilization of the second spider and feeding by the initiator of the encounter.

Results for *Lycosa rabida*.—Two kills occurred among well-fed spiders (days 8 and 21) and three among underfed spiders (days 2, 14, and 16). None were observed directly. The frequency of cannibalism was independent of hunger level.

Results for *Lycosa helluo*.—Two kills occurred among well-fed spiders (days 8 and 11) and two among underfed spiders (days 6 and 28), none directly observed.

In all three species studied, feeding occurred after each kill; however, total consumption did not occur in a single feeding bout. In well-fed groups, where dead spiders were not removed, one spider was observed feeding on the carcass of its victim on three successive days. Scavenging by other spiders also was observed on the day following a kill.

DISCUSSION

Intraspecific Agonistic Interactions.—Richman (1982) found that agonistic display in male salticid spiders contained fewer species-specific elements than did courtship display, as one would anticipate, because the latter is involved in reproductive isolation. In the present study, a number of behaviors occurring during agonistic encounters of *Lycosa* spp. were common to all three species. Based on Aspey's (1977a) demonstration of a signal function for comparable leg raises in male lycosids, it is likely that certain of these actions have a similar role in females. On the other hand, Eberhard (pers. comm.) suggests that some of these behaviors in lycosids may simply be interrupted attack or flight behaviors, rather than special signals which evolved to convey information. He regards it as unlikely that behaviors shown both in attacks on prey and in intraspecific interactions evolved in a communicatory context, since the spider would not want to send any messages to its prospective prey. However, this view does not preclude the possibility that spiders detect such predatory elements in conspecifics and use that information as a basis for terminating an approach.

Much variability occurs in the sequences of behaviors during encounters between female conspecifics; furthermore, there are no obvious differences in the overall types and sequences of response among the three species of *Lycosa* examined. Riechert (1978) points out that a varied repertoire of behaviors probably is adaptive, so-called "protean displays" being used by some species as a defense against predators (Humphries and Driver 1967, 1970). Riechert had extended this hypothesis to the context of territorial disputes in the funnel-web spider *Agelenopsis aperta* (Gertsch), and the same explanation may apply in lycosid spiders. If so, responding to Approach with a varied sequence of behaviors may elicit a halt in Approach or a Retreat from an opponent through the element of surprise.

The large number of Retreats in response to leg raises performed by an opponent reflects the apparent effectiveness of leg raises in inhibiting closer Approach. The number

of Retreats effected by Approach alone probably is a function of the size of the opponent, as assessed by the approached spider. Immediate Retreat also characterizes the spider's response to the approach of a large prey item.

Although too few data are available for a tentative conclusion, the occasional occurrence of injury or death during a Grapple suggests that fighting behavior in female *Lycosa* is semi-ritualized. It is fully ritualized in male *Lycosa rabida*, which do not kill other males during a Grapple (Rovner 1968b). On the other hand, some cases of cannibalism by females occurred in our study when the spiders were not oriented face-to-face, i.e., when a spider was approached laterally or posteriorly. Here cannibalism may well involve a predator-prey interaction. Indeed, it is probable that an initial predatory response to a moving conspecific may be carried to completion if no inhibitory identifying signal is provided by that conspecific.

The flattening response following action that terminates an encounter may be an anti-predator defense. Immobility and the assumption of a more two-dimensional form may make a lycosid spider cryptic in the field.

That tolerance exists in grouped adult female conspecific lycosids of certain ages is clear from our study. Behaviors that inhibit approach and/or attack by other females probably function as spacing mechanisms in the field, serving to maintain interindividual distances and to reduce the possibility of being cannibalized. As indicated in the next section, some of the responses toward conspecifics may have a broadly anti-predator function, being used against any predatory species that approaches or attacks (M. Robinson pers. comm.).

Interspecific Agonistic Interactions.—The behaviors that maintain interindividual distances between conspecifics are also effective against heterospecifics during most interactions. When attacks on heterospecific spiders do occur, they resemble the predator-prey interactions seen when a lycosid captures insect prey (Fig. 7).

The low levels of attack behavior among heterospecifics in our study may be partly due to age or seasonal factors; it may be that more predation on heterospecific adult lycosids occur in females between the final molt and the age of oviposition, when food needs are greatest. Unfortunately, our data on interspecific interactions were collected from spiders whose activity periods had been artificially extended into the winter for this part of our overall investigation. Additional research is necessary to establish whether the high degree of tolerance we observed is typical of pre-reproductive adult females as well. However, it is also possible that the latter females would instead risk fewer attacks, since they have more to lose (in terms of future reproduction) than older females (W. Eberhard pers. comm.; Williams 1966).

Hungry versus Sated Spiders.—As had been determined for an adult salticid (Jackson 1980) and an adult agelenid (Riechert 1981), intraspecific predation was not a response to presumed increased hunger, under the conditions we established in our lycosids. Since spiders are well-adapted to long periods of food deprivation (Anderson 1974), a hungry spider may not be any more likely to risk preying upon a similar size conspecific than is a sated spider. Furthermore, because of its possibly reduced fighting potential, it might even be less likely to attack (W. Eberhard pers. comm.). On the other hand, Eberhard (pers. comm.) points out that the number of cannibalisms occurring in all parts of our study was probably far lower than the number of attempted cannibalisms, since the spiders seem able to defend themselves.

Whereas most spiders in our study were not observed engaging in cannibalism, several cannibalized more than once each. Perhaps some individuals have an advantage over

others due to higher levels of aggressivity. Dominance shown by an individual must depend on more than just size difference, which we had controlled in our groupings by using like-sized individuals. Experience may be an important factor, since Parker (1978) noted that success in previous encounters can increase the readiness for escalation. Indeed, we observed that isolated spiders that fail to capture large or very active insect prey subsequently show timidity to any but small prey items.

Field studies by Edgar (1969) and Hallander (1970) indicated that members of the lycosid genus *Pardosa* C. L. Koch utilize a wide variety of prey, including other spiders. Greenstone (1978) found that *Pardosa ramulosa* (McCook) in the field tend to maintain a balanced diet of varied prey species rather than switch to the most abundant prey. Perhaps whatever level of cannibalism there is among adult wolf spiders in the laboratory results partly from the nutritionally narrow diet of only one or two prey species during the long period of confinement. Future studies of agonistic behavior and cannibalism in spiders should include analyses of the possible roles of diet and of experience in determining the outcome of encounters between adult females.

ACKNOWLEDGMENTS

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**LYCOSA CARBONELLI, SP. NOV.; UNA ETOESPECIE
SIMPÁTRIDA, SIBILINA DE LYCOSA THORELLI
(KEYSERLING) (ARANEAE, LYCOSIDAE)¹**

Fernando G. Costa y Roberto M. Capocasale

División Zoología Experimental
Instituto de Investigaciones Biológicas Clemente Estable
Av. Italia 3318, Montevideo, Uruguay

ABSTRACT

A new species, *Lycosa carbonelli*, is indicated as a sibling species of *Lycosa thorelli* (Keyserling), which is fully described. Both species differ clearly by their patterns of courtship behavior. On the basis of four experiments it was proved that the females only responded receptively in presence of a conspecific male.

RESUMEN

Una especie nueva, *Lycosa carbonelli*, es indicada como especie gemela de *Lycosa thorelli* (Keyserling), la cual es redescrita. Ambas especies difieren claramente por el modelo de su comportamiento sexual. Sobre la base de cuatro experiencias fue probado que las hembras solamente respondieron receptivamente ante la presencia de un macho coespecífico.

INTRODUCCION

En zoología, uno de los trabajos más interesantes es la investigación de especies crípticas. Como dijo Mayr (1968:53): "Apenas hay monografía o revisión taxonómica que no aporte nuevos ejemplos de especies gemelas" Los modelos de comportamiento, como "caracteres clave" para clasificar dichas especies (etoespecies), fueron frecuentemente utilizados.

Concretamente, para las arañas Lycosidae, la literatura registra siete aportes recientes: Hollander y Dijkstra (1974), Uetz y Dondale (1979), Uetz y Denterlein (1979), Suwa (1980), Capocasale (1980), Costa (1980) y Stratton y Uetz (1981).

En este estudio la realidad de la existencia de especies gemelas se basa en la siguiente definición: "poblaciones naturales similares o idénticas morfológicamente que se reproducen aisladamente" (Mayr 1968:49).

El objetivo de este artículo es caracterizar dos especies de arañas pertenecientes al complejo o grupo *Lycosa thorelli* (Keyserling) (Capocasale, en preparación). Se trata de dos especies sibilinas, simpátridas, cuyo aislamiento reproductor se probó por experimentos mixiológicos y que fueron netamente separables por su comportamiento sexual.

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Los estudios citogenéticos de algunas especies de este grupo (Postiglioni y Brum-Zorrilla 1981), indicaron que se trata de especies cuyo complemento cromosómico está constituido por cromosomas telocéntricos, siendo su número diploide $2n = 20 + x_1 x_2 0$ (machos) y $2n = 20 + x_1 x_1 x_2 x_2$ (hembras). Algunos individuos presentaron sin embargo un sistema sexual $x_1 x_2 x_3 0$.

Una vez conocidas las características biológicas que separaron las dos especies sibilinas, fue imprescindible hallar algún carácter morfológico que las diferenciara, con el fin de conocer a cuál pertenecía el holotipo de *L. thorelli*. Un conjunto de pelos amarillos presentes en el tarso de la pata I del macho de *L. thorelli*, inexistentes en *L. carbonelli*, se consideró es un carácter diferencial definitivo, que pasa desapercibido si no se estudian diferencias morfológicas con lentes que superen los 100 aumentos.

MATERIAL Y METODOS GENERALES

Todos los especímenes procedieron de Malvín, Montevideo, Rep. O. del Uruguay. Se colectaron en total 80 especímenes en estado adulto o inmaduro avanzado, en el mismo hábitat (bajo piedras rodeadas de pasto), en el período julio-setiembre de 1977 y de 1980.

La cría en el laboratorio fue individual y la alimentación consistió en larvas de *Tenebrio* sp.

En total se utilizaron 35 machos y 40 hembras. Cada espécimen fue individualizado con un número (que no tiene ninguna relación con el número de colección que le correspondió cuando fue depositado en el Museo Nacional de Historia Natural, Montevideo). Los machos fueron aislados visualmente 20 horas antes de la observación. Cada observación duró 15 min, exceptuando los casos donde hubo cópula. Se dispuso de los especímenes que ya habían intervenido en una experiencia luego de 44 horas de aislamiento. Todos los individuos que intervinieron en las experiencias mixiológicas se utilizaron en las experiencias intraespecíficas. Las experiencias fueron registradas cinematográficamente y el film analizado cuadro a cuadro, quedando el mismo depositado en la División Zoología Experimental del IIBCE. La temperatura durante las experiencias varió entre 22°C y 25°C; la luz fue de 1100 lux, proveniente de tubos fluorescentes. Demás detalles sobre mantenimiento, procedimiento y terminología fueron similares a los de Costa (1975, 1979).

La hipótesis de trabajo fue: "Existen dos especies diferentes, separadas por barreras etológicas." Consecuentemente, en una primera instancia se hizo la separación y la determinación de las especies intuitivamente. Se le llamó a una especie *Lycosa thorelli* (por considerarse que coincidía mejor con la descripción de dicha especie, hecha por Keyserling, 1877) y a la otra *Lycosa* sp. 2 (ver comentarios en *L. thorelli*). Finalmente, se utilizó el comportamiento sexual como instrumento definitivo para separar las dos especies y se empleó la descripción de cada modelo específico como carácter diagnóstico.

EXPERIENCIAS MIXIOLOGICAS

Machos en arena limpia.—Se colocaron 10 machos de *L. thorelli* y 10 machos de *Lycosa* sp. 2 sobre arena extraída a 50 cm. de profundidad (= limpia), con el objetivo de observar el comportamiento de los machos de ambas especies en ausencia de estímulos sexuales, y poder evaluar las posibles alteraciones que se producirían en las dos experiencias siguientes.

Tabla 1.—Diferencias entre los comportamientos sexuales de *Lycosa carbonelli*, sp. nov., y *Lycosa thorelli* (Keyserling) observados en el laboratorio.

Comportamiento sexual	<i>Lycosa carbonelli</i> , sp. nov.	<i>Lycosa thorelli</i> (Keyserling)
Fase primera precopulatoria	Desplazamiento casi continuo	Desplazamiento alternado con pausas
Fase segunda precopulatoria	Desplazamiento lento	Desplazamiento muy rápido
	Actividad continua	Actividad alternada con pausas largas
	Ausencia de desplazamiento "explosivo"	Presencia de desplazamiento "explosivo"
	Semejanza entre fase primera y fase segunda precopulatorias	Distinción radical entre fase primera y fase segunda precopulatorias
Cópula	Presencia de agitación	Ausencia de agitación
	Presencia de oscilación de patas I en 50% de hembras	Ausencia de oscilación de patas I en hembras
	77.8% de las hembras se desplazan con macho arriba	Las hembras no se desplazan en la cópula
	5.6% de las hembras quedaron catalépticas	62.5% de las hembras quedaron catalépticas
	Duración de la cópula: 36.2 ± 10.4 min (N = 18)*	Duración de la cópula: 57.1 ± 17.7 min (N = 16)*

*El test de Student mostró diferencias significativas entre las duraciones de las cópula de ambas especies: $t = 4.13$; $p < 0.001$.

Resultados.—Los machos de ambas especies cumplieron unidades de comportamiento habituales, principalmente quietud y desplazamiento de dirección cambiante.

Machos sobre arena con feromona sexual de hembras de la otra especie.—Se colocaron hembras durante 20 horas en los recipientes, retirándolas inmediatamente antes de la observación. Se ubicaron 10 machos de *L. thorelli* sobre arena con feromona sexual de hembras de *Lycosa* sp. 2 y 10 machos de *Lycosa* sp. 2 sobre arena con feromona sexual de hembras de *L. thorelli*, para observar el comportamiento de los machos ante la feromona sexual heteroespecífica.

Resultados.—Los machos de ambas especies cumplieron al comienzo de la observación algunas unidades de comportamiento sexual (ver caracterización más adelante); su duración fue muy breve.

Machos sobre arena y hembras heteroespecíficas.—Veinte horas antes de la observación se ubicaron las hembras en los recipientes con arena. Luego se ubicaron 10 machos de *L. thorelli* y 10 machos de *Lycosa* sp. 2 ante hembras de la otra especie. La finalidad fue observar el comportamiento de los machos de ambas especies ante las hembras heteroespecíficas.

Resultados.—Los machos de ambas especies realizaron unidades de comportamiento sexual sólo al comienzo del experimento. Las hembras rehuyeron de los machos o los amenazaron. Los machos disminuyeron la intensidad del cortejo, rehuyeron de las hembras e intentaron escapar del recipiente.

Discusión.—Los resultados anteriores confirmaron la hipótesis de trabajo. Fundamentalmente se evidenció la existencia de dos especies sibilinas que en ningún momento se curzaron. En términos etológicos, es de destacar una cierta “confusión” transitoria de los machos respecto a feromona y hembra heteroespecíficas y la relativa tolerancia de las hembras respecto a los machos de la otra especie. También importa el hecho que, aunque ambas especies están en simpatría se separan por barreras reproductoras muy fuertes, probablemente etológicas (ver más adelante).

EXPERIENCIAS INTRAESPECIFICAS

En total se pusieron a copular 69 especímenes, incluidos los intervinientes en las experiencias mixiológicas. Cada espécimen se probó con otro del sexo opuesto, con el fin de averiguar si copulaban. El test se consideró positivo únicamente cuando se cumplió la cópula.

Resultados.—Se obtuvieron 41 cópulas experimentales. Los especímenes se segregaron en dos grupos de parejas.

Discusión.—La separación de los especímenes confirmó la existencia de dos grupos biológicos naturales o especies. Cada grupo mostró un modelo de comportamiento sexual característico y distinto al del otro grupo. Como una de estas especies no está descrita, se justificó la creación de una especie nueva, *Lycosa carbonelli*, caracterizada en principio por su modelo de comportamiento sexual. luego morfológicamente.

Cabe agregar que las hembras fecundadas experimentalmente hicieron ootecas, de las cuales salieron arañas sin particularidades.

Lycosa carbonelli, sp. nov.

Fig. 1, 2

Etimología.—La especie se dedica al entomólogo uruguayo Ing. Agr. Carlos S. Carbonell.

Diagnosis.—Esta especie se diferencia de *Lycosa thorelli* porque el macho carece del conjunto de pelos amarillos microscópicos en el tarso de la pata I (Fig. 2-3) y, fundamentalmente, en el comportamiento sexual (Tabla 1).

Comportamiento sexual.—A. Fase primera precopulatoria: Ante la feromona sexual femenina, el macho de *L. carbonelli* realiza inicialmente movimientos verticales con los palpos semiflexionados, de forma que contactan suave y alternadamente sobre el sustrato (detección). La detección se va confundiendo con un golpeteo más regular de los palpos, que mantienen el ángulo fémoro-patelar aproximadamente en 90°; este unidad de comportamiento (tamborileo) tiene una frecuencia aproximada de 10 golpes por segundo (5 para cada palpo). Posteriormente el macho se mueve lentamente (desplazamiento), en forma continua y cambiando frecuentemente de dirección. Durante el desplazamiento realiza movimientos complejos con las patas I (agitación). En esta unidad de comportamiento se pueden distinguir tres componentes: i) oscilaciones sagitales lentas, con las patas extendidas o semiflexionadas, barriendo un sector no mayor de 50° y donde intervienen todas las articulaciones de la pata I; ii) movimientos laterales de poca amplitud, generalmente con la pata extendida; iii) vibraciones sagitales rápidas (5 por segundo, para cada pata). Los componentes ii y iii se cumplen durante las oscilaciones lentas (i); las dos patas pueden moverse simultáneamente o no. El animal mantiene básicamente el modelo



Fig. 1.—*Lycosa carbonelli*, sp. nov., holotipo macho (N° 750; MNHN Montevideo).

1

de desplazamiento con agitación, intercalándose detecciones (en zonas de mayor densidad de seda de la hembra) seguidas de tamborileo y ocasionalmente oscilaciones sagitales del abdomen (vibraciones abdominales). Otras dos unidades de comportamiento aparecen esporádicamente: tanteo, que consiste en movimientos de las patas anteriores extendidas, de forma que los extremos tarsales contactan repetidamente con el sustrato, y frotamiento, donde las patas I y II homolaterales, semiflexionadas, se frotan entre sí rápidamente.

B. Fase segunda precopulatoria: Después de ver o tocar a la hembra (huyendo en este último caso hasta unos 10 cm), el macho de *L. carbonelli* permanece tendido inmóvil por 10 s o más (quietud). Algunos machos tamborilean previamente y otros inician directamente el modelo básico de la fase, que consiste en desplazamiento lento con agitación, en dirección de la hembra. La actividad es continua, intercalándose algunas detenciones muy breves donde pueden observarse tamborileo, vibraciones abdominales y frotamiento. A medida que se aproxima a la hembra, el macho avanza más lentamente y la agitación y el tamborileo son más intensos.

La actividad de la hembra receptiva consiste en: a) detención con taxia hacia el macho; b) tendimiento sobre el sustrato; c) “acomodo”, variando la posición adoptada al tenderse; d) oscilación alternada de las patas I extendidas (observada sólo en el 50% de las hembras); e) actividades inespecíficas (locomoción, amenaza, huida, etc.). Si la hembra se mueve, el macho queda en quietud brevemente. La monta puede ocurrir luego del primer contacto o después de numerosos retrocesos y avances del macho cortejante.

C. Cópula: La monta la realiza el macho adelantándose ligeramente y suavemente sobre la hembra tendida. La posición adoptada es la típica de los licósidos (posición II según Gerhardt 1924). El macho se inclina sobre un lado y con una pata I separa la pata IV de la hembra y con la otra pata I separa el abdomen de la misma. El macho estira el palpo e inserta el émbolo, observándose numerosas eyaculaciones sin extraer el émbolo. Estas eyaculaciones se exteriorizan por la ingurgitación de la hematódocha y la erección de espinas. Al comienzo de la inserción se observan eyaculaciones cada 2 s, pero luego se

van espaciando gradualmente. Finalizada la inserción de un palpo, el macho lo extrae y cambia de lado. Las patas I intercambian posiciones e inserta el otro palpo, eyaculando repetidamente como con el primero. Después cambia de lado y así sucesivamente hasta cumplir un total de aproximadamente 10 inserciones, de las cuales las 4 primeras ocupan el 80% de la duración total de la cópula. En las últimas inserciones se observan eyaculaciones únicas. Esporádicamente, el macho realiza movimientos de tipo masticatorio sobre los palpos.

El 78% de las hembras realizaron, cerca del final de la cópula, avances "torpes" de locomoción, trasladando el macho hasta 10 cm. Los machos tamborilean y vibran el abdomen durante este traslado, moviendo las patas I y IV hasta retirarse (entre 10 y 15 s de iniciado el movimiento de la hembra). La duración de la cópula de *L. carbonelli* fue de 36.2 ± 10.4 min (18 cópulas controladas), correspondiente a una temperatura de $23.3 \pm 0.8^{\circ}\text{C}$. No se observó persecución por parte de la hembra. Una hembra permaneció cataléptica durante 15 s.

Material típico.—URUGUAY: Montevideo; Malvín, mayo 1977 (F. Costa). Holotipo macho y 10 machos y 12 hembras paratipos depositados en el Museo Nacional de Historia Natural, Montevideo.

Nota.—Se omite la descripción morfológica por considerarse innecesaria. Más adelante se da una redescrición de *L. thorelli*, cuyos caracteres sirven también para *L. carbonelli*.

Lycosa thorelli (Keyserling 1877)

Fig. 3-6

Tarentula Thorellii Keyserling 1877:650, t.I, f. 28; 1891:257, t. 10, f. 194a.

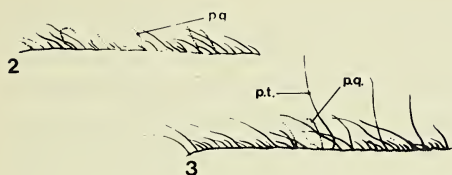
Lycorma thorelli: Roewer 1954:267.

Lycosa thorelli: Bonnet 1957:2629; Zimber 1963:19-21, 23-24, f. 9-10; Capocasale 1980:65-66; Costa 1980:67-68.

Diagnosis.—Esta especie es gemela de *L. carbonelli*; por lo tanto ver diagnosis en *Lycosa carbonelli*, sp. nov.

Comportamiento sexual.—A. Fase primera precopulatoria: Ante la feromona sexual coespecífica, el macho realiza detección (semejante a *L. carbonelli* = SLC) inmediatamente, y luego permanece en quietud por un período muy variable. Se suceden después: detección, tamborileo (SLC; frecuencia 12 golpes/s) asociado a veces con vibraciones abdominales (SLC, más frecuentes e intensas) y desplazamiento lento multidireccional. Durante el desplazamiento se observa la unidad de agitación (SLC, con las siguientes variaciones: a) oscilaciones sagitales más rápidas, que radican principalmente en las articulaciones del trocánter; b) movimientos laterales "rasantes"; c) vibraciones sagitales de frecuencia 6 por segundo, para cada pata). El modelo básico de la fase es de desplazamiento lento con agitación; en un comienzo se intercalan detecciones. El desplazamiento con agitación se interrumpe frecuentemente con la sucesión: tamborileo - quietud - tamborileo - desplazamiento con tanteo (SLC) - desplazamiento con agitación. Estas detecciones se efectúan principalmente en acúmulos de seda femenina, intercalándose muchas veces frotamientos (SLC, aunque más rápidos y con frotamiento de patas II y III homolaterales algunas veces).

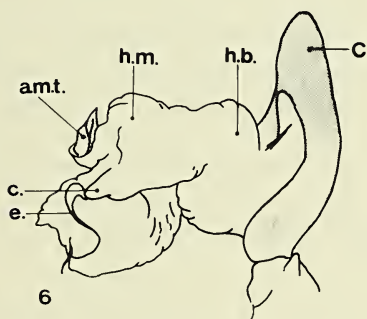
B. Fase segunda precopulatoria: Después de ver o tocar a la hembra, los machos huyen y quedan quietos por unos 30 s. Algunos machos realizan frotamientos intensos. Posteriormente, los machos de *L. thorelli* realizan el modelo básico de esta fase, consistente en



Figs. 2-3.—Esquemas de un perfil dorsal del tarso de la pata I: 2, *Lycosa carbonelli*, sp. nov.; 3, *Lycosa thorelli* (Keyserling). La diferencia entre los distintos tipos de pelos que cubren dicho artejo es significativa. *L. thorelli* tiene un conjunto de pelos muy largos que se suponen táctiles (p. t.) ausentes en *L. carbonelli*. Ambas especies tienen en común los pelos presuntamente quimiosensitivos (p. q.).



Figs. 4-6.—*Lycosa thorelli* (Keyserling) sintipos (N° 2600-26515; British Museum [Natural History]): 4, epigino; 5, espermatecas; 6, bulbo extendido. C = cymbium, a.m.t. = apófisis mesial del tegulum; h.b. = haematodocha basal, h.m. = haematodocha mesial, c. = conductor, e. = émbolo.



la alternancia de quietud extensa (60 s) y desplazamiento “explosivo.” Esta última unidad de comportamiento está formada por avance muy rápido hacia la hembra, que se inicia bruscamente y durante el cual el macho agita las patas I elevadas y extendidas; puede detenerse muy cerca de la hembra o realizar un “choque” con ella, luego del cual queda en quietud con el par I elevado. La duración del desplazamiento “explosivo” no supera 1 s. Frecuentemente esta unidad va precedida por tamborileo de frecuencia creciente y vibraciones abdominales; estas dos unidades pueden observarse también luego del desplazamiento “explosivo”. El modelo se mantiene, hasta que la monta sustituye al “choque.”

La hembra receptiva realiza: a) Detención y taxia hacia el macho; b) tendimiento sobre el sustrato; c) amenaza ante los primeros “choques” y relativa pasividad luego; d) actividades inespecíficas (SLC). Si la hembra se aleja, el macho prolonga el desplazamiento “explosivo” y acorta la duración de la quietud.

C. Cópula: El macho monta a la hembra tendida mediante un salto corto. Se ubica y realiza una dinámica copulatoria básicamente similar a *L. carbonelli*. Las peculiaridades son las siguientes: a) las primeras eyaculaciones duran 1.5 s; b) las segundas inserciones de cada palpo son muy extensas, ocupando ellas solas el 80% de la duración de la cópula; c) las inserciones fueron 6 ó 7, siendo las últimas muy rápidas y de 1 ó 2 eyaculaciones cada una; d) la duración de la cópula fue: 57.1 ± 17.7 min (N = 16 cópulas controladas), correspondiente a una temperatura de $24.1 \pm 1.3^{\circ}\text{C}$.

El 63% de las hembras de *L. thorelli* permanecieron catalépticas durante un promedio de 2.4 min luego de la retirada del macho, mientras que el resto de las hembras reinició su actividad de inmediato, sin perseguir al macho.

Comentarios.—Comparando los comportamientos sexuales de *L. carbonelli* y *L. thorelli*, se observan semejanzas estrechas en la fase primera precopulatoria y en el modelo básico de la cópula, mientras que existen diferencias notorias en la fase segunda precopulatoria y en algunos aspectos de la cópula (Tabla 1). Por lo tanto, la fase segunda precopulatoria (o cortejo propiamente dicho) debe considerarse como fundamental para caracterizar las especies (etoespecies). La segregación total observada entre ambas especies en las experiencias mixiológicas contrasta con las cópulas de casi todos los individuos en los enfrentamientos intraespecíficos, tratándose de los mismos individuos en las mismas condiciones ambientales. Los distintos modelos de cortejo posiblemente sean los responsables directos del aislamiento reproductor observado entre estas especies gemelas y simpátridas. Su eficacia como barrera reproductora se justifica por la ausencia aparente de otra barrera precopulatoria entre ellas. Las semejanzas morfológicas y biológicas en general entre *L. carbonelli* y *L. thorelli* indicarían su estrecho parentesco (grupo *L. thorelli*).

Macho.—Largo total: 9.00 a 10.50 mm (15 especímenes medidos). Cefalotórax: largo 4.25 a 5.60 mm (4.97 ± 0.36); ancho 3.11 a 4.17 mm (3.79 ± 0.43) (20 especímenes medidos); áreas laterales castaño oscuro, mancha submarginal continua amarillo claro; bordes laterales negro; área mediana amarillo claro (Fig. 1). Esternón: amarillo, mancha mediana (1/3 del ancho total del esternón) negro. Quelíceros: castaño naranja. Patas: amarillo, tarso de la pata I con un conjunto de pelos amarillos muy claros (Fig. 3). Abdomen: dorsal castaño, área cardíaca castaño negro bordeada lateralmente de amarillo; áreas laterales diseño reticulado castaño negro sobre fondo amarillo; ventral amarillo. Bulbo: como el esquema de la figura 6.

Hembra.—Largo total 9.68 a 14.72 mm (12.01 ± 1.15). Cefalotórax largo: 4.62 a 6.84 mm (5.73 ± 0.61); ancho 3.66 a 5.23 (4.22 ± 0.43) (20 especímenes medidos). Estructura general semejante al macho. Tarso de la pata I sin pelos amarillos. Epigino y espermatecas como los esquemas de las figuras 4 y 5.

Comentarios.—En el material típico, que consta de cuatro sintipos, el macho se designó como lectotipo (*Lycosa thorelli*); los tres paralectotipos restantes (hembras), deben ser nominados como grupo *Lycosa thorelli* (Mayr, Linsley y Usinger 1953; Mayr 1978), dado que es imposible saber si copularían con el lectotipo.

Los especímenes utilizados en las experiencias mixiológicas como *L. thorelli* (por ajustarse mejor a la descripción de Keyserling) y *Lycosa* sp. 2 fueron mal determinados. Se ignoró la existencia del carácter de los pelos amarillos de la pata I de los machos, jerarquizado posteriormente a las experiencias mixiológicas. Los especímenes indicados allí como *L. thorelli* son en realidad *L. carbonelli*, mientras que los indicados como *Lycosa* sp. 2 son *L. thorelli*. El mismo error de determinación se cometió previamente en Capocasale (1980), Costa (1980) y Postiglioni y Brum-Zorrilla (1981).

Material examinado.—COLOMBIA: "Nueva Granada" (sic); 1890.7.1 (Keyserling) cuatro sintipos (1 macho, 3 hembras) depositados en el British Museum (Natural History). Diecinueve machos y 23 hembras de Uruguay: Montevideo, Malvín; may. 1977 - ago 1980 (F. Costa) depositados en el Museo Nacional de Historia Natural, Montevideo.

Distribución conocida.—Norte de Colombia y sur de Uruguay.

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LARVAL BEHAVIOR AND PHYLOGENETIC
RELATIONSHIPS AMONG SCORPIONS

Alberto Ugolini and Marco Vannini

Istituto di Zoologia dell 'Università
via Romana 17
50125 Firenze, Italia

ABSTRACT

The larvae of two species of *Euscorpium* (Chactidae) were each allowed to settle on the backs of immobilized adults of 8 species of scorpions belonging to 4 families. The percentage of larvae still present after 12 hours was recorded. A significant correlation appeared between these results and the phylogenetic relationship, as suggested by Lamoral (1980),between *Euscorpium* and the other families.

INTRODUCTION

The larvae of *Euscorpium carpathicus* (L.) and *E. flavicaudis* (Geer) settle on the backs of congeneric adult scorpions regardless of their species, sex or reproductive phase (Vannini et al. 1978, Vannini and Ugolini 1980). The mother-larva bond is regulated not only by specific behavior of both the larva and the mother but also by tactile (Angermann 1957, Vannini et al. 1978) and chemical (Vannini and Ugolini 1980) cues. The reaction of two species of *Euscorpium* larvae to adults belonging to different families is the object of this paper.

Table 1.—Species tested.

Family	Species	Locality
Chactidae	<i>Euscorpium carpathicus</i> (L.)	Italy
	<i>Euscorpium flavicaudis</i> (Geer)	Italy
Scorpionidae	<i>Scorpio maurus fuscus</i>	Israel
	(Hemprich & Ehrenberg)	
	<i>Pandinus pallidus</i> (Kraepelin)	Somalia
Diplocentridae	<i>Nebo hierichonticus</i> (Simon)	Israel
Buthidae	<i>Buthotus polystictus</i> (Pocock)	Somalia
	<i>Buthotus judaicus</i> (Simon)	Israel
	<i>Leiurus quinquestriatus</i>	Israel
	(Hemprich & Ehrenberg)	
	<i>Androctonus crassicauda</i>	Israel
	(Olivier)	

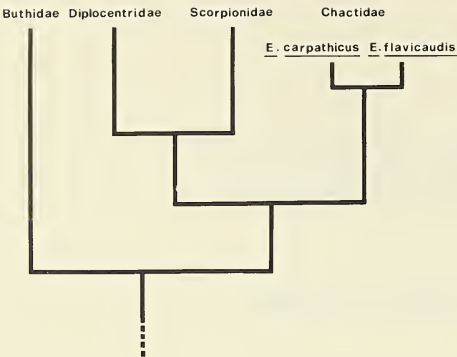


Fig. 1.—Cladogram of the scorpion families, adapted from Lamoral (1980). Three families not tested in our experiments have been omitted.

MATERIALS AND METHODS

Gravid *E. carpathicus* and *E. flavicaudis* females were collected in the vicinity of Florence and raised in the laboratory. Upon birth the larvae were placed in groups of ten on the backs of live, immobilized (see Vannini et al. 1978) adult scorpions (8 species representing 4 families: Table 1). None of these adults gave birth before or after the experiments. The number of larvae still present on the back of each adult was recorded 12 hours later. Each group of larvae was tested once. All the experiments were conducted in complete darkness, at room temperatures and RH, in September-October 1981.

RESULTS AND DISCUSSION

The number of *Euscorpius* larvae available daily was irregular and unequal for both species. Thus, the results of Table 2 are somewhat unbalanced.

A preference hierarchy for both species of *Euscorpius* was obtained (Table 2, columns P_c and P_f). Applying the Spearman rank correlation test to these hierarchies shows a high correlation between the two species ($r_s = 0.983$; $P < 0.01$). Pooling the data of both species gives their average preference hierarchy for the adults of other families (Table 2, column P_a).

Table 2.—Number of larvae still on the back of adults of various species after 12 h: in brackets, number of adults; N_c and N_f , number of larvae tested; P_c and P_f , percentage of settled larvae; P_a , average percentage.

<i>Euscorpius carpathicus</i>				<i>E. flavicaudis</i>				
			N_c	P_c		N_f	P_f	P_a
E.f.	(4)	10 9 10 10 10	50	98.0	9 10 9 9 10 10 9 10 10 9 10 9 10	130	95.4	96.1
E.c.	(4)	10 10 8 9 9 10 10 10	80	95.0	8 10 10 9 9 9 9	70	91.4	93.3
S.m.	(3)	10 9 6 9 9 9	60	86.7	10 6 10 6 10 9 8 10 9 8	100	86.0	86.2
P.p.	(1)	8 10 6 5	40	72.5	9 5 10	30	80.0	75.7
N.h.	(3)	2 2 5 9 5 7	60	50.0	6 9 9 1 8 10 1 5 10 10	100	69.0	61.9
B.j.	(3)	0 5 4 10 9 8	60	60.0	7 10 7 8 10 9 9 4 1 0	100	65.0	63.1
B.p.	(2)	0 10 10 2 7 3	60	53.3	5 5 0 8 5 0 0 0 1 0	100	24.0	35.0
L.q.	(3)	0 0 0 3	40	7.5	0 0 8 2 0 0 0 0 1 0 0 0	120	9.2	8.7
A.c.	(1)	1 0 0	30	3.3	0 1 0 0 0 0 5 2 0	90	8.9	7.5

Table 3.—Comparison between hierarchy of phylogenetic relationship (Fig. 1) and settling preference (Table 2, P_a).

Species	Family	Number of Branchings	Rank	Settling Preference
<i>Euscorpis</i> (homospecific)	Chactidae	0	1	1
<i>Euscorpis</i> (heterospecific)	Chactidae	1	2	2
<i>S. maurus fuscus</i>	Scorpionidae	2	4	3
<i>P. pallidus</i>	Scorpionidae	2	4	4
<i>N. hierichonticus</i>	Diplocentridae	2	4	6
<i>B. polystictus</i>	Buthidae	3	7.5	7
<i>B. judaicus</i>	Buthidae	3	7.5	5
<i>L. quinquestriatus</i>	Buthidae	3	7.5	8
<i>A. crassicauda</i>	Buthidae	3	7.5	9

The hierarchy of settling preference derived from our experiments (Table 3, $r_s = 0.879$; $P < 0.01$) agrees with the cladogram proposed by Lamoral (1980) for the various families of scorpions (Fig. 1). The slight discrepancies in behavior of the two species of *Euscorpis* could be due to experimental error. Of interest is the fact that, after considering congeneric affinities, the larvae showed a distinct preference for the Scorpionidae ($z = -1.97$; $P < 0.025$; Mann-Whitney U test) although these and the Diplocentridae show the same cladistic distance from the Chactidae. Among the Buthidae, the larvae preferred *Buthotus* to the two other genera ($z = -5.98$; $P < 0.001$; Mann-Whitney U test).

It has already been demonstrated that prolonged permanence of scorpion larvae on the mother's back is based on chemical and physical grounds (Vannini et al. 1978, Vannini and Ugolini 1980, 1981). A chloroform extract of the mother's cuticle prepared on blotting paper proved to be attractive to the larvae (Vannini and Ugolini 1980). It is possible that the relationship between phylogenetic position and settling preferences shown by the larvae is due to the differences in the wax making up the epicuticular layer, which is partially removable in chloroform and chloroform:methanol (see Hadley and Jackson 1977, Toolson and Hadley 1977, 1979, Vannini and Ugolini 1980).

In strictly taxonomical terms our methods are rather approximate and therefore we cannot expect a precise relationship between settling preference and taxonomical position. However, since there appears to be a general correlation between the two, at least at the family level, our technique does provide a positive and integrative contribution to present taxonomical knowledge of scorpions, especially if reciprocally experiments were to be carried out (i.e. Buthidae, Diplocentridae and Scorpionidae larvae on Chactidae adults), and extended to other families.

Torres and Heatwole (1967) used a similar technique to discover the factors regulating settling on maternal back, and their results do not seem in contrast with a general applicability of the method. They tested Buthidae larvae on Diplocentridae, Scorpionidae and Buthidae females. Although the larvae settled almost exclusively on conspecifics, it should be noted that the adults were not immobilized, only a small number of larvae were used, and some of the offspring were tested in the nymphal stage.

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RELATIVE ABUNDANCE OF THREE VAEJOVID SCORPIONS ACROSS A HABITAT GRADIENT

Richard A. Bradley¹ and Allison J. Brody

Department of Biology
University of New Mexico
Albuquerque, New Mexico 87131

ABSTRACT

Relative abundance of three vaejovid scorpions was assessed using pitfall traps. Scorpions were sampled west of Albuquerque, Bernalillo Co., New Mexico during summer 1982. A total of 146 scorpions was captured in 3735 trap nights. *Paruroctonus utahensis* was the dominant species in flat grassland habitat (62-72% of captures). *Vaejovis coahuilae* and *V. russelli* were both found in the flat grassland habitat, but in lower numbers than *P. utahensis*. The two *Vaejovis* species were common in rocky cliff habitat (*V. coahuilae* 61%, *V. russelli* 37%) but *P. utahensis* was rare on the cliff (2% of captures). *Paruroctonus* may be unable to occupy the rocky cliff because it lacks suitable soil for burrowing.

INTRODUCTION

Three species of scorpions of the family Vaejovidae occur in the desert grasslands around Albuquerque, Bernalillo County, New Mexico. Two of the species are congeners, *Vaejovis coahuilae* Williams and *V. russelli* Williams; the third species is *Paruroctonus utahensis* (Williams). All three species are strictly nocturnal, and may be found on warm nights between March and November.

West of Albuquerque there is a gradual plain with sandy loam soil interrupted by a basalt cliff. The plain above the cliff slopes down to the east at about 2.6% to the cliff edge at an elevation of about 1616 m. The cliff drops about 30 m (25% slope) to a bajada (7-10% slope) then another gradual plain (3-5%). Above the cliff there exists a desert grassland composed primarily of mesa dropseed (*Sporobolus flexuosus*), galleta (*Hilaria jamesii*), black grama (*Bouteloua eriopoda*), and rice grass (*Oryzopsis hymenoides*). There are also widely scattered shrubs, primarily snakeweed (*Gutierrezia sarothrae*), indigobush (*Dalea scoparia*), four-winged saltbush (*Atriplex canescens*) and soapweed yucca (*Yucca glauca*). The vegetation below is similar to that above the cliff, but is dominated by rice grass and indigobush. The vegetation on the cliff-face is a sparse community similar in composition to the surrounding plains.

Initial observations indicated that the two *Vaejovis* species were most common on the rocky slope, and less so above and below this area. *Paruroctonus*, however, was most often observed on the flat grassland habitat. During the summer of 1982 a trapping

¹ Current address: School of Biological Sciences, University of Sydney, Sydney, 2006, NSW, Australia.

program was conducted to determine the relative abundances of these three species along this habitat gradient. Pitfall traps were used to capture scorpions. Unfortunately pitfall traps introduce several potential biases in sampling. First the more mobile species tend to be overrepresented in the pit samples. Secondly sampling was destructive, in that scorpions were removed from the area, potentially reducing population levels of the rare species. For this reason, additional data from nocturnal observations using a portable ultraviolet light have been included in the analysis.

METHODS

We buried 19 pitfall traps (470 ml plastic cups) flush with the soil surface along a transect running down the cliff-face. Ten were located between basalt boulders on the cliff-face, and the remainder were installed on the bajada below. An additional transect (19 pitfalls) was installed on the flats below the cliff. Traps were checked once every 2-3 days and all captured scorpions were removed and returned to the laboratory for identification. Scorpions captured in a pit grid 2 km N of this locality (above the cliffs) were also included in the analysis. The pit transects were sampled between 7 June and 8 August 1982. In addition to the pitfall capture data, we have included information on relative abundance obtained using a portable UV light. Black light samples were obtained between 25 May 1981 and 22 November 1982.

RESULTS

A total of 146 scorpions was captured in 3735 trap nights. *Paruroctonus utahensis* was the most common scorpion captured in the pits located on the flats above (72%) and below (61%) the cliff-face (Fig. 1). *Vaejovis coahuilae* outnumbered *V. russelli* in both flatland samples (Fig. 1). In contrast, *P. utahensis* constituted only 2% of the scorpions captured on the cliff-face (Fig. 1). *Vaejovis coahuilae* comprised 61% and *V. russelli* 37% of the cliff-face sample. The species proportions on the rocky slope are statistically different from those on the flats ($P < 0.001$, G-test; Sokal and Rohlf 1981). The differences between the two flatland samples are not statistically significant.

Information from black light surveys of these habitats confirm the pattern of segregation by habitat. Of 1837 scorpions located in the flatland habitat, 1646 or 90% were *Paruroctonus utahensis*. *Vaejovis coahuilae* comprised 7% of the sample (= 128 scorpions) and *Vaejovis russelli* made up only 3% of the total (63). The fact that this sample is more heavily biased toward *Paruroctonus* is undoubtedly due to the fact that blacklighting is not influenced by the differential mobility of the species. In limited blacklight sampling of the rocky slope habitat, only one individual of *Paruroctonus* was located, compared to 19 *V. coahuilae* and 11 *V. russelli*.

DISCUSSION

Clearly, *P. utahensis* exhibits a habitat occupancy pattern that is nearly the reverse of that of the *Vaejovis* species. Both *Vaejovis* species are found in burrows, under rocks, or under wood during the day. On the other hand, *P. utahensis* usually lives in a deep spiral burrow in the soil. The absence of *P. utahensis* on the cliff-face is possibly due to a lack of suitable burrow sites. There is evidence that some species of scorpions may be limited

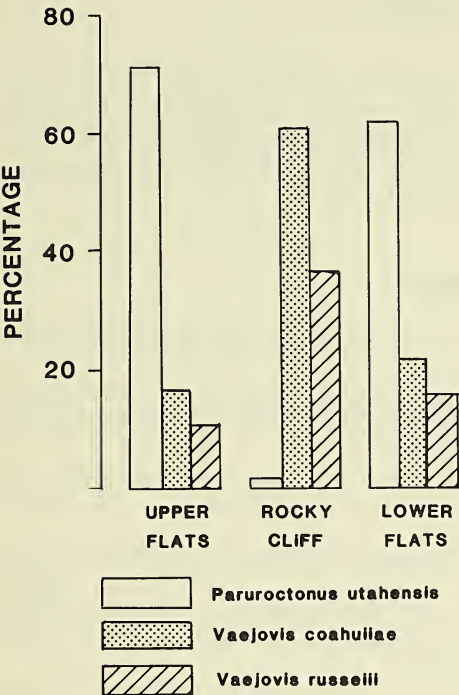


Fig. 1.—Proportions of the scorpion species captured in pitfall traps west of Albuquerque, New Mexico. The upper and lower flats samples were taken from relatively flat grassland habitat. The differences between these two flatland sites was not statistically significant. The rocky cliff sample was highly significantly different from the flatland samples ($P < 0.001$, G-Test).

by soil conditions for burrowing (Lamoral 1978). The soil present on the cliff face is often shallow (10-15 cm). *Paruroctonus* constructs burrows in the flatland habitat that are frequently deeper than 20 cm. Habitat segregation among scorpions into rock inhabiting forms and soil inhabiting forms has been reported before (Hadley and Williams 1968), Williams 1970, Koch 1978).

There are several possible explanations for the decreased numbers of *Vaejovis* on the flats. One is that cliffs represent better habitat for the two *Vaejovis* species studied here. A second is that both *Vaejovis* species are excluded from the flatland habitat by competition with *P. utahensis*. These three species may compete exploitatively. Williams (1970) indicated that the two main factors permitting coexistence between scorpions in the Phoenix South Mountain area were probably habitat specialization and differential prey preference. Whether differential habitat occupancy between the two *Vaejovis* species studied by Williams was the result of past competitive interactions is unknown. There is some overlap in prey eaten by the three sympatric scorpions (Bradley, pers. obs.). The answer to the question of exploitation competition must await quantitative analysis of the resource base that is presumed to be limiting.

We have observed interspecific predation among these three scorpion species. *Vaejovis russelli* eating a juvenile *Paruroctonus utahensis*, *P. utahensis* eating young *V. coahuilae* (2 occasions), and *V. coahuilae* eating a young *V. russelli*. All three species overlap widely in size, and small individuals are subject to cannibalism as well as predation by the other scorpion species. Interspecific predation may represent a potent form of interference competition among scorpions (Polis et al. 1981). Proof that interference competition influences the distribution of these three scorpions will require analysis of population regulation in these forms.

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***LUBINELLA*, A NEW GENUS OF ULOBORIDAE (ARACHNIDA, ARANEAE)**

Brent D. Opell

Department of Biology
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061

ABSTRACT

The new genus *Lubinella* from New Guinea is described and illustrated and its relationship discussed.

INTRODUCTION

Owing to its prominent eye tubercles, the new genus *Lubinella* appears upon first examination to be related to *Sybota* and *Orinomana*. However, the presence of a single pair of female spermathecae and of a male palpal femoral tubercle and median apophysis bulb unite this genus with *Uloborus*, *Zosis*, *Purumitra*, *Octonoba*, *Conifaber*, *Ponella*, *Philoponella*, and *Daramuliana*. The synapomorphy of numerous, small, abdominally restricted tracheoles unites *Lubinella* most closely with the latter seven genera. The presence of a weakly sclerotized conductor homolog (or vestigial conductor) arising from the center of the median apophysis bulb (Figs 10, 11) is an apomorphic feature shared with *Zosis*, *Purumitra*, *Octonoba*, and *Conifaber*. Yoshida (1980, 1981, 1982) shows that, like *Lubinella*, many *Octonoba* species lack a tegular spur on the male palpus. For this reason, *Lubinella* appears most closely allied with *Octonoba*. Several *Octonoba* species have an anterior median epigynal lobe which may have extended posteriorly, fusing with the lateral lobes to form the paired crypts and posterior extension characteristic of *Lubinella*.

The web of *Lubinella* has diverged from the horizontal orb-web which appears to be characteristic of *Octonoba* species (Yoshida 1980, 1981). Although this asymmetrical web is still a horizontal or sloping orb, its smaller hemisphere is situated nearer a substrate retreat and incorporates a vacant sector through which one or several signal lines extend (species F, Lubin, in press). Opell (in ms) suggests that eye tubercles of *Lubinella*, like those of *Hyptiotes* and *Miagrammopes* may accompany carapace muscle reorganization associated with monitoring a single (signal) line. As in *Miagrammopes*, these tubercles may also extend or otherwise shift the visual field of *Lubinella*. The posterior eyes of *Lubinella* are proportionally larger and their lenses more protuberant than those of the eight genera with which it is most closely allied.

Another striking feature of the genus is the male's apparent use of a groove near the apex of the narrow cymbium (arrows, Figs. 8, 11) as an embolus guide. Although a

similar function has been suggested for the broad cymbial lobe of *Tangaroa* species (Opell 1979, 1983), *Lubinella* is the only uloborid group with a distinct cymbial groove in which the apically directed embolus can lie. As a result of critical-point-drying the embolus shown in Figs. 10 and 11 pulled away from the palp's apical region. Both prior to preparation and upon return to alcohol the embolus tip was adjacent to cymbial tip and median apophysis spur as shown in Fig. 8. Examination of an expanded palp indicates that the apically-curved distal embolic region rests in the cymbial groove, its outward movement perhaps restricted by the protruding tip of the vestigial conductor. The flattened, twisted median apophysis spur appears to hook under the epigynum's posterior rim, securing the palpus and allowing the reduced median apophysis bulb to articulate with one of the epigynal crypts.

Lubinella, new genus

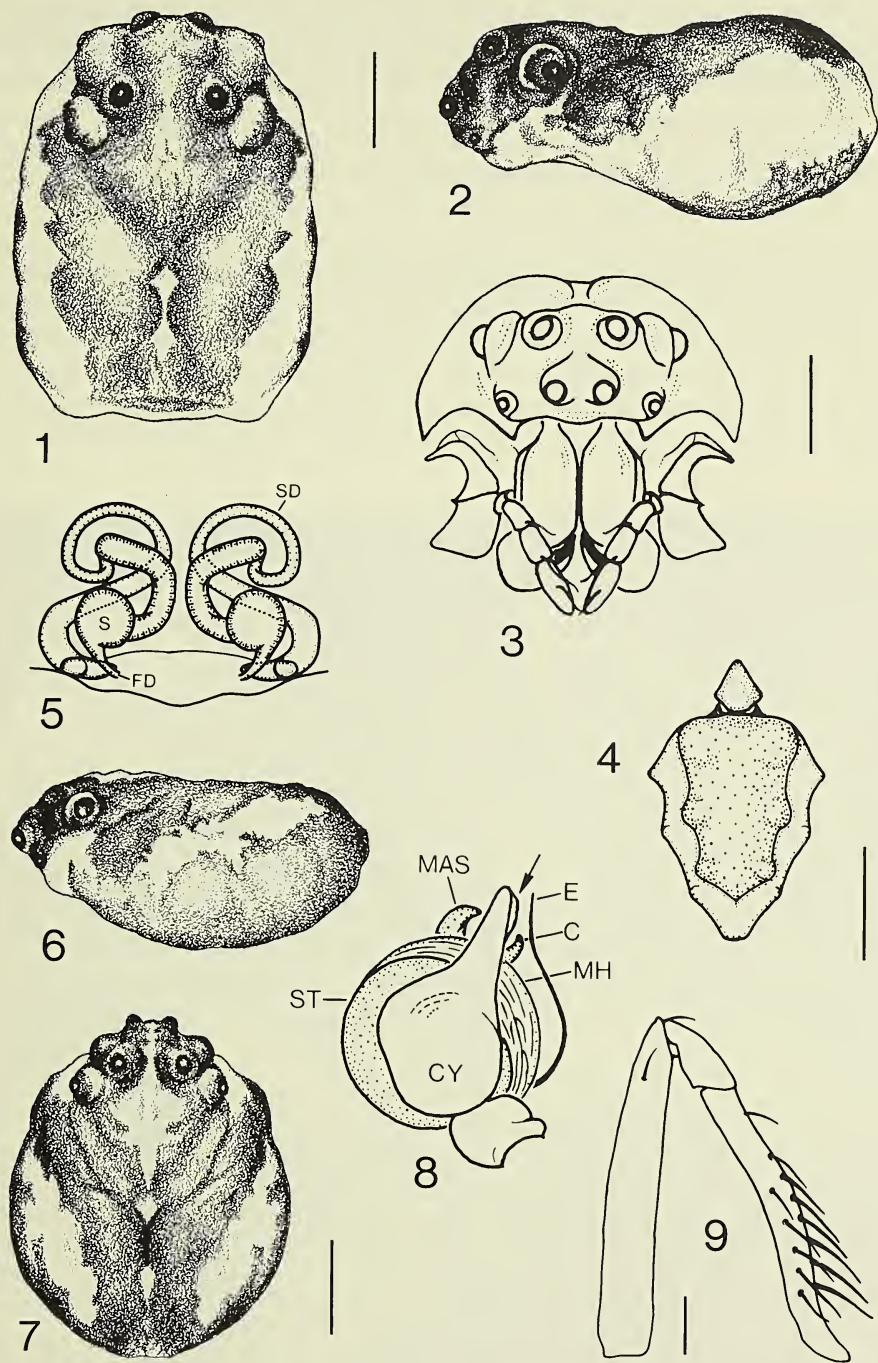
Figs. 1-13

Type.—The type species of this genus is *Lubinella morobensis*, new species. The feminine name is an arbitrary combination of letters denoting the taxon's collector (in lieu of a strict, but preoccupied, patronym).

Diagnosis.—Females are distinguished by the presence of prominent eye tubercles (Figs. 1-3) and a divided, ventral epigynal crypt with a posterior rim that overhangs a depression of the epigynum's posterior plate (Fig. 11). Although *Sybota* and *Orinomana* also have eye tubercles (Opell 1979, figs. 100, 115, 121) their epigynae do not have paired ventral crypts. *Philoponella divisa* Opell has a weakly divided transverse epigynal crypt (Opell 1979, fig. 221) and *Daramuliana* separated longitudinal crypts with a posterior median scape (Opell 1979, fig. 189), but neither taxon has prominent eye tubercles, posterolateral epigynal openings, nor a posteriorly protruding epigynal rim. Males are also distinguished by conspicuous eye tubercles (Figs. 6, 7) and by a palpus which has a narrow cymbial tip (Fig. 8), a small median apophysis bulb, a broad, twisted median apophysis spur, and a triangular, weakly sclerotized conductor homolog (Figs. 10, 11). *Conifaber*, *Purumitra*, and *Zosis* male palpi also have a vestigial conductor (Opell 1979, plates 6-c, 7-c, d; Lubin et al. 1982, figs. 14, 15), but are characterized by a tegular spur not present in *Lubinella*.

Description.—Female. Carapace more rectangular than that of most uloborids, maximum width 0.8 length, width at PLE 0.7 length. Cephalic region slightly elevated and laterally set off from rest of carapace (Figs. 1, 2). All eyes on tubercles. When viewed dorsally both eye rows recurved, anterior so that lines across AME posterior margins passes across ALE anterior margins, posterior so that lines across PME posterior margins passes one-half diameter anterior to PLE foremargins. Clypeus height equal to AME diameter (Fig. 3). Length and posterior width of median ocular area twice its anterior width. Lateral ocular rectangle half as long as wide. Width of endite 0.70 length, of labium 0.95 length. Raised central sternum region with bulge adjacent to each coxa (Fig. 4). Femur I 1.9 carapace length. Total leg length ratio (I:II:III:IV): 1.0: 0.51: 0.37: 0.67. Calamistrum length about 0.34 metatarsus IV length and 1.44 cribellum width. Abdomen without dorsal tubercles or posterior extension. Maximum width and height equal, 0.52-0.66 length. Details of genitalia (Figs. 5, 12, 13) provided in species description.

Male. Carapace suboval, maximum width 0.9 length, width at PLE 0.8 length. Deep thoracic groove. Cephalic region more conspicuously set off than in males of related taxa, but not so abruptly as in female (Figs. 6, 7). Eye arrangement, endite and labium propor-



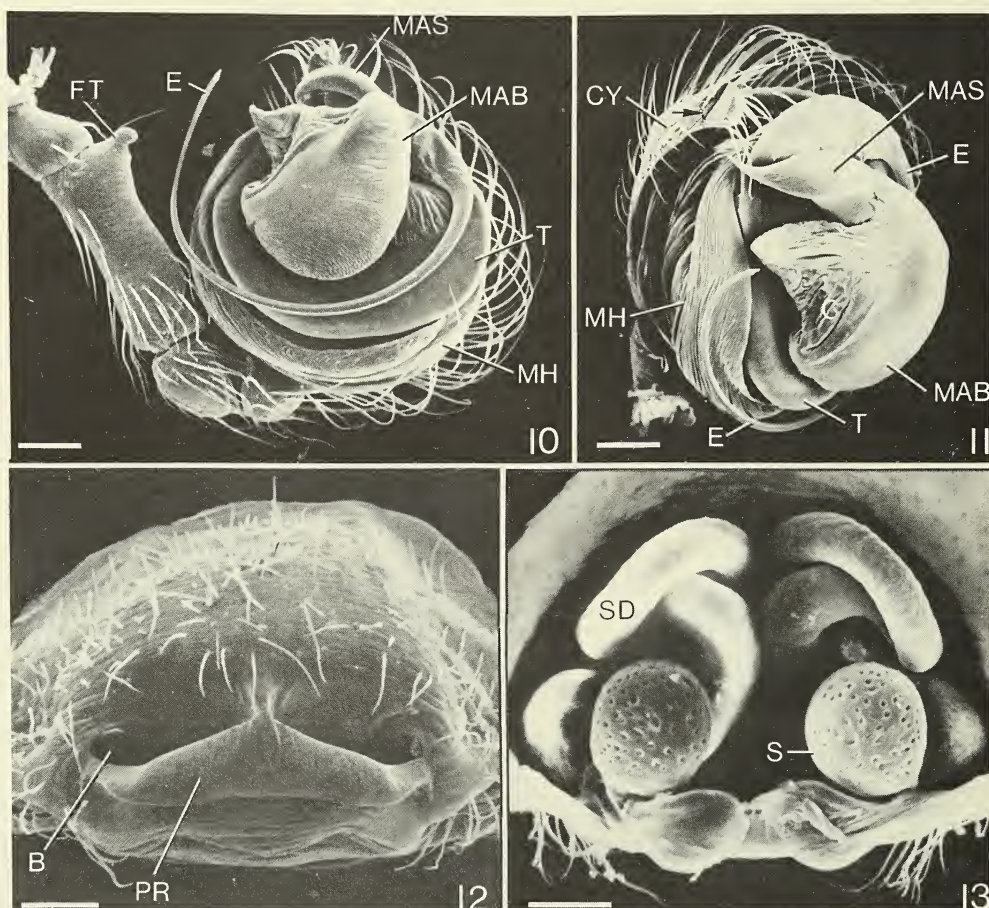
Figs. 1-9.—*Lubinella morobensis*, n. sp.: 1, Dorsal view of female carapace; 2, Lateral view of female carapace; 3, Anterior view of female; 4, Female sternum; 5, Dorsal view of cleared epigynum (FD = fertilization duct, S = spermatheca, SD = sperm duct); 6, Lateral view of male carapace; 7, Dorsal view of male carapace; 8, Prolateral view of male left palpus showing cymbium (CY) with posterior notch (arrow), subtegulum (ST), middle hematodocha (MH), embolus (E), median apophysis spur (MAS), and vestigial conductor tip (C); 9, Prolateral view of male left first femur, patella, and tibia. All scale bars represent 500 μ m.

tions, and sternum similar to female. Femur I 1.7 carapace length. Total leg length ratio: 1.0: 0.51: 0.37: 0.62. Abdomen without dorsal tubercles, maximum width 0.48 length, maximum height 0.40 length. Palpal details (Figs. 8, 10, 11) provided in species description.

Lubinella morobensis, new species

Figs. 1-13

Types.—All from Morobe Province, Papua New Guinea, collected by Yael D. Lubin. Female holotype and paratype from Merri Creek, above Wau, 2100 m elev., collected 10 Dec. 1979. Female and male paratype from Mt. Missim, 1600 m elev., collected 3 Oct. 1979. Female paratype from Wau Ecology Institute, 1200 m elev., collected 11 Mar. 1980. Latter specimen deposited in American Museum of Natural History, others in the Museum of Comparative Zoology. This species is named for the province in which it was collected.



Figs. 10-13.—*Lubinella morobensis* n. sp.: 10, Retrolateral view of male left palpus; 11, Apical view of male left palpus; 12, Ventral view of epigynum; 13, Dorsal view of cleaned epigynum. CY = cymbium (arrow indicates cymbial notch), E = embolus, FT = femoral tubercle, MAB = median apophysis bulb, MAS = median apophysis spur, MH = middle hematodocha, T = tegulum; B = bursal opening, PR = posterior rim, S = spermatheca, SD = sperm duct. All scale bars represent 50 μ m.

Diagnosis.—This species is, at present, the only one recognized in the genus.

Description.—Female. Total length 5.48-6.47 mm ($N = 4$, $\bar{X} = 6.00$), carapace length 2.00-2.14 mm ($\bar{X} = 2.09$), maximum carapace width 1.60-1.74 mm ($\bar{X} = 1.69$). AME, ALE, PME, PLE diameters 160, 105, 200, 200 μm , respectively. Sternum length 1.10-1.24 mm ($\bar{X} = 1.15$). Chelicerae with 1-2 large apical, 1-2 large basal, and 2-3 small median promarginal teeth and 4-5 small median retromarginal teeth. Carapace dark brown with broad lateral white stripes, narrow longitudinal white stripe on thoracic groove, and white PME tubercles (Figs. 1, 2). PME of alcohol preserved specimens with lavender sheen not reported for other uloborids. Sternum tan with brown rim around periphery of raised central region. Legs brown with narrow white ring on distal quarter of femora, proximal margin and center of tibiae, and proximal margins of metatarsae and tarsae. Femur I 3.80-4.16 mm long ($\bar{X} = 3.99$) with 1 prolateral, 1 dorsal, and 1 retrolateral macroseta. Tibia I with 3-4 prolateral, 2 dorsal, and 2 retrolateral macrosetae. Calamistrum 0.74-0.86 mm long ($\bar{X} = 0.79$), composed of 32-40 setae, spaced 20-23 μm apart. Ventral comb 1.58-1.83 mm long ($\bar{X} = 1.74$), comprised of 32-35 tarsal and 5-7 metatarsal setae spaced 42-43 μm apart. Oval abdomen 3.60-4.56 mm long ($\bar{X} = 4.00$). Cribellum 0.53-0.57 mm wide ($\bar{X} = 0.55$ mm). Abdomen light with scattered black pigment forming dark anterior tip and narrow four- or five-lobed dorsal folium. Brown pigment outlines midventral stripe and colors book lungs and anterior epigynal margin. Epigynum with two deep, oval, ventral crypts divided by thin septum (Fig. 12). Each crypt twice as broad as long, with opening at lateral margin which connects to looped sperm duct that increases in diameter and wall thickness near medial connection to spherical posterior spermatheca (Figs. 5, 13). In posterior view epigynum 0.80 as high as broad. Thin, dorsally curved posterior rim forms narrow recess on epigynum's posteroventral surface.

Male. Total length 4.15 mm, carapace length 1.72 mm, maximum carapace width 1.58 mm. AME, ALE, PME, PLE diameters 160, 80, 160, 160 μm , respectively. Sternum length 0.90 mm. Chelicerae with 5-6 small promarginal and 4 very small retromarginal teeth. Carapace dark brown with pair of broad, diverging lateral white stripes, small white spot in and just posterior to thoracic groove, white, median arrow with shaft beginning at AME and tip terminating at thoracic groove; and white patch on either side of lateral ocular area (Figs. 6, 7). PME lavender. Sternum and leg color similar to that of female except metatarsae II-IV light with distal gray ring. Femur I 2.96 mm long, with one prolateral, one dorsal, and no retrolateral macrosetae. Tibia I 2.25 mm long with prominent distal crook, 5 prolateral, 12-13 dorsal, and 2-3 retrolateral macrosetae (Fig. 9). Ventral comb 1.16 mm long with 19 tarsal and 4 metatarsal setae, mean spacing 50 μm . Slender gray abdomen 2.52 mm long with large white hourglass shaped spot in cardiac area posterior to which are large median and three pairs of paraxial white spots. Venter with broad white stripe extending forward between gray book lung covers and becoming laterally darker near spinnerets. Palpal femur with large median and lateral proximal femoral tubercles. Width of distal third of cymbium less than one quarter that of basal region, cymbial tip with posterior groove (Fig. 8, arrow). Median apophysis bulb a small hemisphere with diameter about 0.60 that of tegulum (Figs. 10, 11). Conductor a weakly sclerotized triangular projection. Median apophysis spur thin, twisted, and pointed.

Distribution.—Known only from Morobe Province, Papua New Guinea.

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RESEARCH NOTES

PREDATORS OF TWO ORB-WEB SPIDERS (ARANEAE, ARANEIDAE)

I present direct and indirect evidence of five spider predators on the orb-web spiders, *Argiope aurantia*, Lucas and *A. trifasciata* (Forsk.) I also discuss indirect evidence of avian predation on these spiders. Michael J. Apicella and John Chambarlis made some of the observations on invertebrate predators. David Wise offered helpful criticisms during the preparation of this manuscript, and George Uetz identified the *Schizocosa* for me. Part of this study was supported by a grant (DEB-790491) from the National Science Foundation.

Argiope aurantia and *A. trifasciata* are large spiders (adult females ca 25 and 20 mm respectively) which build nearly vertical orbs in old field and edge habitats throughout North America. Both species overwinter in the egg case and emerge in the late spring. During the summer they increase in size from 1-2 mm up to adult size. Both species usually rebuild their orbs every day, with the exceptions of the periods around molting and egg laying.

Previously recorded invertebrate predators of *A. aurantia* and *A. trifasciata* include Hymenoptera (e.g., Muma and Jeffers 1945, Krombein 1953, Kurczewski and Kurczewski 1968, Marples 1969, Enders 1974), *Phidippus audax* (Hentz) and *P. rimator* (Walckenaer) (Salticidae) (Tolbert 1975), and unidentified lycosid (Enders 1975), an unidentified mimetid (Enders 1974) and congeneric spiders (Enders 1974, Tolbert 1975, Taub 1977).

Birds were suggested as a major group of predators on orb-web spiders (Hingston 1927, Bristowe 1941, Marples 1969), and avian predation on several araneids was observed (Marples 1969, Robinson and Robinson 1970, Royama 1970, Blanke 1972). However, no accounts exist of avian predation on *A. aurantia* or *A. trifasciata*.

The observations presented here were made while studying these spiders at the Smithsonian's Chesapeake Bay Center for Environmental Studies in Edgewater, Maryland, during June through August of 1979 and 1980. The invertebrate predators were encountered while recording data on 8580 unmarked spiders and their webs. The evidence of avian predation resulted from a part of the study which involved marking the spiders and webs and following spider movement on a daily basis. During this portion webs were marked and individuals followed for an average of 5 days each, for a total of 2674 web-days.

Spider predation.—Observations of spider predators are summarized in Table 1. *Phidippus* and *Schizocosa* were observed feeding on *Argiope*. The actual attacks by *Lycosa*, *Oxyopes*, and *Rhomphaea* were not observed, but these species were found sitting head down in hubs of *Argiope* webs (the normal location of *Argiope*). I assume that a wandering spider such as *Lycosa* or *Oxyopes* which is in the hub of an *Argiope* web had attacked and perhaps ingested the original resident. *Rhomphaea lacerta* was previously observed entering the webs of other species and killing the occupant (Archer 1940).

Table 1.—Summary of the observed instances of spider predation on *A. aurantia* and *A. trifasciata*. (* = approximate size, based on web dimensions)

Predator	n	body size in mm.		Prey ID
		predator	prey	
Lycosidae				
<i>Lycosa rabida</i> (Walck.)	8	5-12	3-10*	A.a.
<i>Schizocosa retorsa</i> (Banks)	1	8	2	A.t.
Theridiidae				
<i>Rhomphaea lacerta</i> (Walck.)	2	6,5-7	5-7*	A.t.
Oxyopidae				
<i>Rhomphaea salticus</i> (Hentz)	3	4-6	3-5	A.t.
Salticidae				
<i>Phidippus rimator</i> (Walck.)	2	7,8	6,11	A.a., A.t.

Avian predation.—I did not observe avian predation on these spiders, presumably due to the rarity of the event and the fact that birds are scared away by human observers. However, I encountered a characteristic type of web destruction, consisting of a missing triangular sector beginning in the hub and extending out to the periphery of the orb. I found this type of damage in 15 out of a total of 2674 webs during 1979 and 1980. I believe such damage is due to avian predation. The missing sector usually consists of 1/6 to 1/3 of the web. Occasionally as much as 1/2 of the web is missing. The size of the missing portion varies, but it always begins within the hub, where the spider normally rests. These spiders make new webs essentially every day, and these missing sectors were found in new webs which were otherwise in good condition.

During a laboratory study of avian predators on *A. aurantia* and *A. trifasciata* (Horton 1980), I observed blue jays attacking spiders in their webs. Typically the bird perched adjacent to the web and grasped the spider with a pecking movement. Frequently the bird moved its head laterally after the attack, resulting in the removal of a triangular sector of the web which began at the hub. While in the field during the same study I observed this pattern of web destruction in 9 of 276 webs.

Holes in the center of the web were also found (5 of 2674). This type of damage could have been caused by Hymenoptera or birds. David Wise (pers. comm.) observed that web damage can result from predatory attacks by Hymenoptera on orb-web spiders. A small predator such as a Hymenoptera would probably not cause extensive web damage. The holes could also be caused by a bird pecking at the spider.

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Charles C. Horton, Aberdeen Hall, Harford Community College, 401 Thomas Run Road, Bel Air, Maryland 21014. (Present address: Department of Biology, College of Notre Dame of Maryland, North Charles Street, Baltimore, Maryland 21210).

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NON-GLARE MATERIAL FOR POSITIONING SPECIMENS DURING STUDY

Light colored beach sand is commonly placed in a Stender dish to allow positioning of alcohol preserved specimens while they are being examined or drawn under a dissecting microscope. Although this holds a specimen in the desired orientation, reflections from this light background produce glare. This can be particularly problematic at greater magnifications where glare increases due to the higher light intensity required for proper illumination and combines with reduced depth of field to limit resolution of fine details.

An inexpensive solution to this problem is the use of silicon carbide abrasive powder. The irregular particles of this black material are small enough to allow easy positioning of all but the smallest structures and, although facets of a few particles may reflect light, the net effect is a background with no glare. A few initial rinses are sufficient to remove particles that float to the surface or cloud the alcohol. The only difficulty encountered when using this material is that ocular grid or reticule lines are not easily discernible against the black background.

Silicon carbide abrasive is available from lapidary and hobby shops and is also sold in small packets as a spark plug cleaning abrasive by auto parts, hardware and discount stores.

Brent D. Opell, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061.

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AN ASSOCIATION OF EARWIGS (DERMAPTERA) AND BUGS (HETEROPTERA) IN A SPIDER'S (ARANEAE) WEB?

This paper reports an interesting association of Dermaptera and Heteroptera found in the egg-sac spinning of an African Eresidae spider. In a split of the bark of an *Adansonia digitata* tree (Bombacaceae) of about 3 m diameter the web of a spider was found near Damagum, 204 km W Maiduguri, Nigeria. It was approximately 5 cm wide, 20 cm long and contained in the upper half an egg-sac of about 3-4 cm diameter. Additionally, the web contained a large number of living insects and chitinous remains. It was removed intact for examination and found to contain:

- 130 living specimens of *Forficula senegalensis* Serville (Dermaptera: Forficulidae) (det. Brindle, Manchester);
- 41 living specimens of *Carbula pedalis* Bergroth (Heteroptera: Pentatomidae) (det. Dolling, London);
- 16 living ants of 2.5 - 3.0 mm body length (still undetermined);
- chitinous remains of *Forficula*, *Carbula*, and Coleoptera (2 Chrysomelidae 3.5 mm, 1 Cantharidae 7 mm, 1 unidentified 4 mm, 1 larva 6.5 mm).

The web had apparently been made by *Adonea* sp. (Eresidae) determined by exuviae found in it (det. Heimer, Dresden). The egg-sac contained some 100 eggs with beginning ontogenesis. The web of a theridiid spider was found 30 cm away on the same tree. Prey entangled in the theridiid web included the integral, evacuated exoskeletons of 22 *Carbula*, eight *Forficula*, and numerous chitinous fragments, as well as four undamaged ants.

In the eresid web, bugs and earwigs moved unhindered by the cribellate threads. During the day both were found only here in a dense cluster, and nowhere else on the tree, indicating that they had moved to the web actively and were not entangled as prey insects. Such an association is not known to any of the three taxonomists who determined the species. The biology of these arthropods is largely unknown, and this apparently peaceful coexistence of Dermaptera, Pentatomidae, and spiders (resp. eggs) poses an interesting question.

Carbula is a plant-sucking bug, *Forficula* is probably omniphagous. Some African Pentatomidae and Forficulidae appear sometimes in large numbers, the latter perhaps being migratory. This study occurred during the dry season and all *Adansonia* trees had already lost their leaves, so it seems possible that the insects survive the dry season in such aggregations. The smooth bark structure of the *Adansonia* trees and the surroundings (harvested millet fields) offered hardly any other protected places. Placed in a small split of the bark as it was, the spider's web offered a protection during the day. At night earwigs and bugs walk on the bark near the web, presumably to look for food, probably causing some of them to become entangled in the sticky threads of the nearby theridiid web. Possibly due to the greater mobility of the Dermaptera, the Pentatomidae were captured three times more often than the Forficulidae. The special character of the hackled band cribellate silk of the Eresidae may account for the nearly unimpeded mobility of these insects in it, but since this type of silk is known to be highly effective in entrapping some insects the question remains unanswered.

My thanks are due to Drs. Brindle, Dolling, and Heimer for the identification of the species and to C. Taylor for correcting my English.

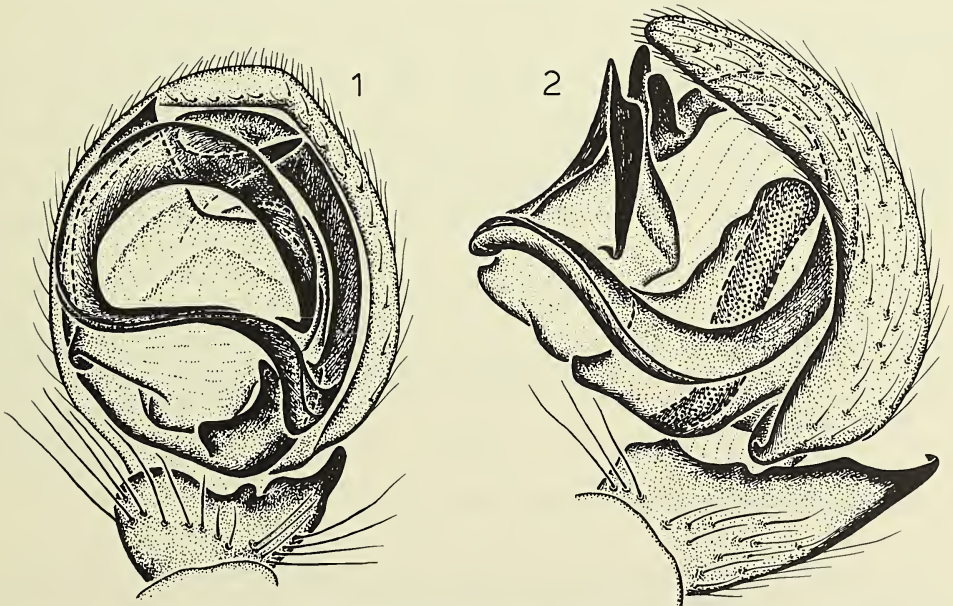
Wolfgang Nentwig, Fachbereich Biologie/Zoologie, Universitat Lahnberge, D-3550 Marburg, West Germany.

ON THE MALE OF *DOLIOMALUS* (ARANEAE, GNAPHOSOIDEA)

INTRODUCTION

The genus *Doliomalus* was established by Simon (1897) for the curious Chilean spider *Delena cimidoides* Nicolet (1849), one of the very few flattened, laterigrade, thomisiform gnaphosoids found in the New World. Two other species have been placed in the genus, but one, the Chilean *D. laminus* (Nicolet), is a *nomen dubium*, and the other, the Central African *D. berlandi* Lessert, proved to be a crab spider rather than a gnaphosoid (Platnick 1976b). Hence *Doliomalus* is at present monotypic, and, although females of *D. cimidoides* have been taken repeatedly over the past century, males have remained unknown. Thus it was with great pleasure that I recently received from Dr. Luis E. Peña of Santiago, Chile, a sample of *D. cimidoides* from Valparaíso Province that included an adult male. The male palp (Figs. 1, 2) is of unexpected complexity, quite unlike those of Asian *Plator* Simon (see Platnick 1976a, figs. 7, 9) or South American *Vectius* Simon, the two other genera that, like *Doliomalus*, have been placed by most authors in the separate family Platoridae rather than in the gnaphosid subfamily Hemicloeiinae. As noted earlier (Platnick 1976a), it is unlikely that the recognition of the classical Platoridae can be supported by adequate phylogenetic arguments.

In the comments on the male that follow, only differences from the description of the female provided by Platnick (1976b) are noted. In addition to specimens in the collection of the American Museum of Natural History (AMNH), specimens were made available by Dr. H. W. Levi of the Museum of Comparative Zoology, Harvard University (MCZ) and Dr. M. Hubert of the Muséum National d'Histoire Naturelle, Paris (MNHN). The illustrations are by Dr. M. U. Shadab of the American Museum.



Figs. 1, 2.—*Doliomalus cimidoides* (Nicolet), male palp; 1, ventral view; 2, retrolateral view.

Doliomalus cimicoides (Nicolet)

Figs. 1, 2

Delena cimicoides Nicolet, 1849:381, pl. 3, fig. 6 (female holotype from Chile, no specific locality, lost).

Plator cimicoides: Simon, 1880:236.

Doliomalus cimicoides: Simon, 1897:19. Platnick, 1976b:978, figs. 5-7.

Diagnosis.—The rounded, rather than semicircular, carapace (Platnick 1976b, fig. 5), together with a massive palpal conductor supporting an elongated and thickened embolus (Figs. 1, 2) in males and a bilobed epigynum with small, sinuous, posterior spermathecae (Platnick 1976b, figs. 6, 7) in females, will separate *D. cimicoides* from the other known flattened gnaphosoids (platorids and hemicloelines).

Male.—Total length, not including chelicerae, 5.15 mm. Carapace 2.14 mm long, 2.32 mm wide between coxae II and III, where widest, orange; posterior margin slightly invaginated at middle; surface coated with scattered weak setae. Anterior median eyes separated by only their diameter from anterior laterals; posterior medians separated by only twice their diameter, by only three times their diameter from posterior laterals. Chelicerae orange, labium and endites light orange. Sternum wider than long (35/34). Coxae IV separated by only about two-thirds their length. Abdomen longer than wide (87/55). Median spinnerets without elongated tips, directed posteriorly, without longitudinal rows of spigots. Femur II 3.44 mm long. Palpal tibia with long, sinuous retrolateral apophysis; embolus long, thick, twisted, heavily sclerotized at edges, originating distally, coiling proximally, supported by massive, distally pointed conductor and long terminal apophysis (Figs. 1, 2).

Female.—Described by Platnick (1976b).

Distribution.—Central Chile, from Valparaíso south to Cautín Provinces.

Material Examined.—CHILE: *Bío-Bío*: Caledonia, June 1975 (L. E. Peña), 1 female (AMNH); *Cautín*: Villarrica, 1 female (MNHN); *Maule*: Cayurranquil, W Cauquenes (400 m, *Nothofagus* forest), 24-27 Jan. 1981 (L. E. Peña), 1 female (AMNH); *Ñuble*: Chillán (1400 m), 3 Mar. 1968 (L. E. Peña), 1 female (MCZ), Las Trancas, Chillán, 20-25 Feb. 1980 (L. E. Peña), 1 female (AMNH), Recinto, SE Chillán (800 m), 23 Jan. 1979 (L. E. Peña), 1 female (AMNH), Tregualemu, 24 Jan. 1976 (G. Moreno), 1 female (AMNH); *O'Higgins*: Caletones, Rancagua, 1946 (L. C. Wood), 1 female (MCZ); *Santiago*: Aculeo, Quebrada del Arbol, Oct. 1959 (L. E. Peña), 1 female (MCZ), El Canelo (800-1400 m), 1980 (L. E. Peña), 3 females (AMNH), El Manzano, Aug. 1931 (I. Olfro), 1 female (AMNH), Quilicura, 25 May 1979 (L. E. Peña), 1 female (AMNH); *Talca*: Alta de Vilches, 31 Oct. 1969 (J. G. Rozen, L. E. Peña), 1 female (AMNH); *Valparaíso*: Cerro Las Vizcachas (1800-2200 m), 1-12 Dec. 1982 (L. E. Peña), 1 male, 3 females, Viña del Mar, 28 Feb. 1977 (A. Tobar), 1 female (AMNH).

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Norman I. Platnick, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.

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ON THE GNAPHOSIDAE (ARACHNIDA, ARANEAE) OF THE CALIFORNIA CHANNEL ISLANDS

By coincidence, I recently received from separate sources a male and a female of the spider genus *Drassyllus*, each collected on the smallest of the California Channel Islands, Santa Barbara. Because the abundant and widespread western species *Drassyllus insularis* (Banks) is known from several other Channel Islands¹, it seemed likely that the Santa Barbara specimens would also belong to that species. As they proved instead to represent a hitherto undescribed form, I take the opportunity here to supplement a recent revision of the genus (Platnick and Shadab 1982) and also to summarize the known records of Channel Island Gnaphosidae.

As indicated below (Table 1), ten species have been collected on at least one of the eight main islands. Eight of these ten species occur also on the adjacent mainland, and most of them are widespread in California, if not all of western North America. The other two species, the new *Drassyllus* described below and *Zelotes cruz* Platnick and Shadab (1983), are (so far as known) Channel Island endemics. Both of these taxa belong to species groups that are speciose in California, but their sister species or groups have not yet been identified with precision, primarily because several species in each group are still known from only one sex.

I am indebted to F. G. Hochberg, W. R. Icenogle, S. E. Miller, M. J. Moody, and M. E. Thompson for sharing specimens and information, and to M. U. Shadab for work on illustrations. The format of the description and abbreviations of morphological terms follow those used in the revision.

Table 1.—Species of Gnaphosidae and the Channel Islands on which they have been collected.

Species	Islands							
	San Miguel	Santa Rosa	Santa Cruz	Anacapa	San Nicolas	Santa Barbara	Santa Catalina	San Clemente
<i>Gnaphosa maritima</i> Platnick and Shadab		+	+		+		+	
<i>Haplodrassus signifer</i> (C. L. Koch)		+			+			
<i>Drassodes angulus</i> Platnick and Shadab				+				+
<i>Herpyllus propinquus</i> (Keyserling)							+	
<i>Nodocion voluntarius</i> (Chamberlin)				+				
<i>Sergiolus montanus</i> (Emerton)	+				+			
<i>Drassyllus insularis</i> (Banks)	+	+	+		+		+	+
<i>Drassyllus barbus</i> Platnick						+		
<i>Zelotes cruz</i> Platnick and Shadab			+	+		+		
<i>Micaria utahna</i> Gertsch							+	

¹*Drassyllus insularis* was originally described from Guadalupe Island, off Baja California Norte, Mexico. The few females available from that island show slight epigynal differences from mainland and Channel Island females. If males can be collected on Guadalupe, they may show the species to be distinct from the widespread population, for which the name *D. irritans* (Chamberlin) would be available.

Drassyllus barbus, new species

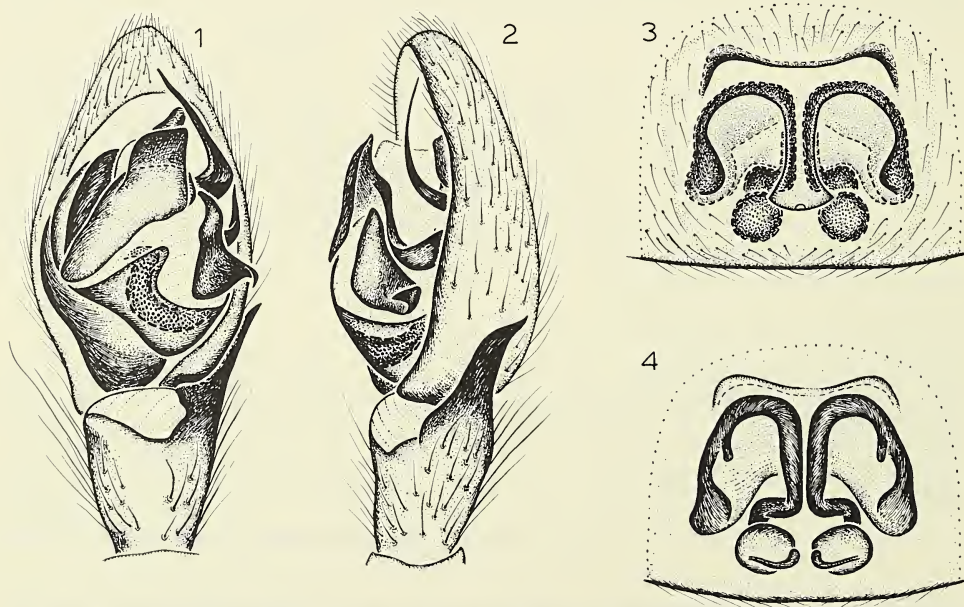
Figures 1-4

Types.—Female holotype collected under a rock on Santa Barbara Island, Santa Barbara County, California (28 March 1982; Martin Galindo-Ramirez), deposited in the American Museum of Natural History courtesy of Mr. Wendell R. Icenogle, and male paratype from the same locality (2-6 April 1979; Scott E. Miller), deposited in the Santa Barbara Museum of Natural History (catalogue number 33888).

Etymology.—The specific name is an arbitrary combination of letters.

Diagnosis.—Males of this species (a member of the *insularis* group) will be identified as *D. fractus* by users of the published key (Platnick and Shadab 1982:73) but can be distinguished from males of that species by the more prolaterally situated terminal apophysis and the narrower embolar projection (Figs. 1, 2). Females will key out to *D. coajus* but can be distinguished from females of that species by having a large flange connecting the anterior and median epigynal ducts (Figs. 3, 4). The only other taxon *D. barbus* is likely to be confused with is *D. ojus*, females of which have a similar epigynum but differ in having the lateral extensions of the midpiece further from the anterior epigynal margin, more strongly curved posterior epigynal ducts, and shorter anterior epigynal ducts.

Male.—Total length 4.18. Carapace 1.79 long, 1.31 wide. Femur II 1.22 long. Eye sizes and interdistances: AME 0.05, ALE 0.07, PME 0.09, PLE 0.10; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.03, ALE-PLE 0.03. MOQ length 0.23, front width 0.16, back width 0.20. TAB with long retrolateral extension; TA prolaterally situated, rounded distally (Figs. 1,2). Leg spination: femur IV p0-1-1; tibia III v2-2-2; metatarsi: I v0-0-0; III r1-2-2.



Figs. 1-4.—*Drassyllus barbus*, new species: 1, palp, ventral view; 2, palp, retrolateral view; 3, epigynum, ventral view; 4, epigynum, dorsal view.

Female.—Total length 5.49. Carapace 2.27 long, 1.99 wide. Femur II 1.51 long. Eye sizes and interdistances: AME 0.09, ALE 0.10, PME 0.12, PLE 0.11; AME-AME 0.04, AME-ALE 0.02, PME-PME 0.03, PME-PLE 0.05, ALE-PLE 0.07. MOQ length 0.31, front width 0.22, back width 0.27. AEM extending almost entire width of epigynum; AED extending to near SP (Figs. 3,4). Leg spination: femur IV p0-1-1, r0-1-1; tibia III v2-2-2; metatarsi: I v0-0-0; III v2-2-0, r1-2-2.

Material Examined.—Only the types.

Distribution.—Known only from Santa Barbara Island, California.

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Manuscript received July 1982, accepted August 1982.

Norman I. Platnick, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024.

BOOK REVIEWS

Brignoli, P. M. 1983. A Catalogue of the Araneae Described between 1940 and 1981. P. Merrett, ed. Manchester Univ. Press, Manchester M139PL, U. K. and Dover, New Hampshire 03820, U. S. A. \$90.00, 755 pages.

This book's checklist of families serves as a reminder of the many recent changes in spider taxonomy. For example, the cribellate-ecribellate distinction is no longer evident and many newly characterized families are present. The work that follows will be a welcome reference for systematists engaged in such research and for others wishing a complete list of all spider families and genera and of the new species described and the nomenclatural changes made since 1940. Following an introduction in which the limits, coverage, and organization of the work are explained, Brignoli comments on nomenclatural and systematical procedures and problems associated with taxonomic publications. Throughout the volume he continues to offer the benefit of his experience with spider taxonomy and taxonomic literature by including short notes on the history, placement, and spelling of taxa whose status is other than routine.

The book follows the scheme of Roewer's *Katalog der Araneae*, giving first a bibliography divided by year and then a catalog with families phylogenetically arranged. A systematic index appears at the front of the volume and an alphabetical generic index at the back, the latter making this catalog compatible with Bonnet's *Bibliographia Araneorum*. The volume is brought up to date by a 58-page, 1979-80 bibliographic and systematic addendum that shares the generic index. Like Roewer, Brignoli omits fossil taxa and introduces a *nomen novum* when he discovers a homonym.

Under each of the 96 families are listed: 1. genera for which no new species have been described since 1940, 2. genera that have been transferred to other families, 3. genera that are now junior synonyms, 4. new species that have been placed in synonymy or homonymy, and 5. genera containing new species or subspecies. Subfamilies are recognized in 13 families, but in the remainder, genera are listed alphabetically. The species of large, widely distributed genera are first geographically divided and then, like those of smaller genera, listed alphabetically. Each species and subspecies entry includes: 1. the sexes known, 2. the author and date of publication, 3. the page on which its description begins, 4. figure references, 5. an indication of whether the citation refers to a complete description or a less complete account such as a generic transfer, 6. the sex of type specimen(s), and 7. the country from which the species was collected. In the case of the United States and Russia, disjunct territories such as Alaska and Caucasus are so designated.

The need for this work is supported by the fact that each of its 104 bibliographic pages contains about 20 entries and each of its 600 catalog pages lists an average of about 16 new species. The thoroughness and organization it achieves will facilitate research and help reduce errors in spider systematics and, by so doing, contribute to advances in all areas of spider biology.

Brent D. Opell, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Dondale, Charles D., and James H. Redner. 1982. The Insects and Arachnids of Canada. Part 9. The Sac Spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae). Agric. Can. Publ. No. 1724. 194 pp. (\$8.95 in Canada, \$10.75 elsewhere). Available from Canadian Government Publishing Centre, Supply and Services Canada, Ottawa, Ontario K1A 0S9.

Ecological, physiological, behavioral, biogeographical, and other works in biology can only be as good as the identifications of the organisms on which they are based. Biologists depend on systematists and systematic publications for their identifications. All arachnologists, then, regardless of their specialties, should welcome this second volume on the spiders of Canada and Alaska. This work covers two families of two-clawed hunting spiders, Clubionidae and Anyphaenidae.

The organization and format are similar to those of the previous contribution on the crab spiders (Dondale and Redner 1978). The section on anatomy (1 1/2 pp.) largely repeats the anatomy section in "The crab spiders. . ." but deals more specifically with sac spiders. Some detail on the families and genera is deferred to discussions of those groups. Inclusion of this section should be valuable for the novice who may not have the previous volume on hand. Sections on techniques, classification, and a key to families are omitted.

Keys are provided in both English and French to the eight genera and 66 species of Clubionidae and three genera and six species of Anyphaenidae found in Canada. Descriptions of the families, genera, and species are clearly written, but I found the diagnoses (under "Comments") redundant, repeating the information in the keys. The 339 figures (black and white line drawings) by Redner are large, clear, and well labeled. These include ventral and lateral views of male palpi and external and internal views of epigyna. Internal views were often omitted in older works, so these, especially, should aid identification of these species. Geographical ranges in and near Canada are illustrated on 52 maps, and complete ranges are given in the text. A glossary (5 pp.), lists of references (5 pp.), and index to names (2 pp.) complete the volume.

Editing and printing are generally well done; I am aware of only one misspelling in the text (I'm not going to tell you where). Figures 258-265 are out of order (following 266-274), an incorrect symbol for *Anyphaena pectorosa* appears in the caption to Map 51, and the dots on Map 52 are unnecessarily small. Although these are minor irritations, they cause no confusion.

What this reviewer misses, however, is a more critical discussion of the characters that define these families. The definition of sac spiders (p. 10, paragraph 3) includes seven characters, all primitive for the group; in other words, sac spiders are defined by the derived characters they lack! Anyphaenidae is well defined, following Platnick (1974) and Platnick and Lau (1975), by the advanced placement of the tracheal spiracle, the large tracheal trunks with tracheae extending into the prosoma, and the lamelliform claw tuft setae, but a critical definition of Clubionidae is needed. Is Clubionidae a polyphyletic group as suggested recently (Lehtinen 1967, Forster 1970, Platnick 1974, Platnick and Lay 1975)? Or, if the clubionids form a monophyletic group, what derived character do they share? These questions go unanswered here and elsewhere.

Even if these questions of classification were answerable, an identification manual is not the best place to introduce a new classification. As an identification manual this book succeeds very well. Every arachnologist working in Canada and the northern U. S. should find it valuable.

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Andrew J. Penniman, Department of Zoology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210.

Robinson, M. H. and B. Robinson, 1980. Comparative Studies of the Courtship and Mating Behavior of Tropical Araneid Spiders. Pacific Insects Monograph No. 36, 218 pp. Bishop Museum, Honolulu. \$22.50.

This book-length monograph on araneid sexual behavior is obviously a labor *of* as well as being about love. From the high quality photographs to the careful detail of the descriptions, from the range of side topics touched upon (the alarming world-wide shortage of taxonomists, the habitats and webs of the species studied, male kelptoparasitism on females) to the patience I know from personal experience was necessary to see all that they saw, and to the very observations themselves ("massive, massive high intensity tugging, . . . vigorous pulling, it's a magnificent slow motion tug, . . ."), the authors' excitement and enjoyment of the study shines through. The Robinsons continue the admirable tradition, established with their work on attack behavior and *Nephila*, of giving rounded, summary views of what they have seen rather than splitting off pieces to publish as separate papers. This makes for longer papers (and shorter curriculum vitae), but means each paper is a gold mine to be visited again and again. In fact the broad survey nature of this work, reflecting the Robinsons' unusually wide travels in the tropics, is not likely to be duplicated in the near future, and they are undoubtedly destined to go down as the Masters and Johnson of araneid sexual behavior.

The monograph's basic aim was the detection of behavioral differences between higher order groups of araneids, and to this end the Robinsons observed 53 species in 15 genera in two of Simon's subfamilies (Nephilinae, Argiopinae), and found and categorized 18 major types of male behavior. The accounts of their observations make up the bulk of the text. It is difficult to know in a pioneering work like this which kinds of observations will prove useful and in what contexts they will be used, so the detailed nature of the descriptions is justified. As M. Robinson has written elsewhere, watching araneids court without being able to monitor the vibrations they produce is like watching a symphony orchestra play without hearing any sound; this simile dramatizes the possibly limited nature of their data. The overall patterns of variation in behavior are then summarized and discussed. What emerges is puzzling. There are clear groups of species which share entire suites of characters, but contrary to expectations, the groupings do not follow taxonomic lines

(there is at least one species of *Argiope* or *Gea* in each of the three major groups). The Robinsons' tentative attempt to trace the evolutionary sequence of the development of these suites is somewhat unconvincing; in particular they lack observations of related groups such as tetragnathines, metines, theridiosomatids, theridiids, metids, etc. (filling this gap would make a nice thesis project). Other surprises are the relative lack of variety in male behaviors (perhaps the variety of vibrations produced is greater), and the apparent lack of stereotypy in the order and duration of the behaviors the males perform. I had supposed, reasoning from the assumption that male courtship functions to isolate different species reproductively, that each species would have a distinct male courtship code; the authors wisely stop short of trying to assess the value of male courtship in preventing interspecific mating, but I suspect the other two functions they discuss — reduction of predatory drive and arousal of the female (i.e. sexual selection by female choice) — may be very important. A final note on the substance of what they saw concerns the anomalous behavior of *Mecynogea*; the taxonomic position of this genus with the strange sheet web is even less clear than it was before.

The production of the monograph is excellent, and there are very few errors of any sort. The price is not unreasonable for a specialized work of this sort.

William G. Eberhard, Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

ON YET ANOTHER ARTIFICIAL SPIDER CLASSIFICATION: A REVIEW

Levi, Herbert W. 1982. Araneae. In Parker, Sybil B. (ed.), *Synopsis and Classification of Living Organisms*. McGraw-Hill Book Company, New York, vol. 2, pp. 77-95.

Levi's 1982 classification of spiders is presented as part of a two-volume survey of the families of living organisms that includes coverage of scorpions (by O. F. Francke), pseudoscorpions (by W. B. Muchmore), solpugids (by M. H. Muma), opilionids (by W. A. Shear), and acari (by D. E. Johnston and others); the smaller orders are covered in short accounts by Levi. The spider section is worthy of note primarily because it contains a new classification and descriptions of families that are offered to the general public as a summary of our knowledge of the order. Unfortunately, it is so riddled with errors of fact and analysis that one can only hope the general public is never misled by it. Since the volumes carry a hefty price tag (\$150), their distribution will probably be limited to libraries.

Levi acknowledges at the beginning that "family classifications are controversial"; although one might expect, therefore, to find many families placed only *incertae sedis*, such is not the case—all the families of araneomorphs discussed are assigned to one of 16 equally ranked superfamilies. Levi indicates that "a conservative view is used here," by which he evidently means that classical groups which are known to be artificial are retained at the expense of more recently proposed groups that might possibly be natural.

The most obvious instance of this is Levi's superfamilial classification of araneomorphs. Evidence available in the literature since at least 1968 indicates that the fundamental division within the Araneomorphae is between a group (Palaeocribellatae) containing only the two genera *Hypochilus* and *Ectatosticta* and a group (Neocribellatae) containing all other araneomorphs. But Levi retains the archaic lumping of *Hypochilus* and *Ectatosticta* with *Hickmania*, *Gradungula*, and *Thaïda* in the single superfamily Hypochiloidea, a clearly artificial group defined only by the absence of the derived characters that unite all other araneomorphs. One could understand the deceptive allure of "A/not-A" grouping, but in this case Levi does not even recognize the corresponding "A" group, the Araneoclada!

Even those systematists who can tolerate groups that are probably paraphyletic are likely to balk at groups that are probably polyphyletic, such as Levi's superfamilies Eresoidea (containing the Uloboridae, Dinopidae, and Eresidae) and Palpimanoidea (containing the Zodariidae, Mecysmaucheniidae, Palpimanidae, and Stenochilidae). The Eresoidea is *presented* as a wastebasket group: "The three families . . . are not closely related but do not fit into other groups." The Palpimanoidea are united because "the posterior spinnerets are reduced or lost." The homology of the condition of the spinnerets in the Zodariidae to that in the other families is doubtful; even Levi says that "The loss of the posterior spinnerets, although unique, is a poor characteristic upon which to base common origin." The cause of his reservations about the group seems to be the fact that some of the families are haplogyne whereas others are entelegyne (i.e., have an epigynum, in Levi's terminology). Levi claims twice that the zodariids and mecysmaucheniids have an epigynum, but in fact the mecysmaucheniids do not. In this case again, Levi has retained an archaic association (between zodariids and true palpimanoids), which even he suspects is artificial, in preference to an alternative one (between zodariids and corinnids) already presented in the literature (by Lehtinen, 15 years ago) that is probably correct.

Those systematists who do search for natural groups will be dismayed to find that Levi's desire to have a neat series of pigeonholes (suborders and superfamilies) in which to stick families has led him to ignore all evidence that some of those suborders and superfamilies may even (horrors!) have interrelationships. For example, Levi recognizes three suborders (Mesothelae, "Orthognatha," and Labidognatha) but does not specify which of the other two suborders his orthognaths are most closely related to. Similarly, Levi distributes the classical Haplogynae among four superfamilies (Dysderoidea, Caponoidea, Scytodoidea, and Pholcoidea) but never informs the reader that the latter three superfamilies are united by having lamellate chelicerae. And for the mygalomorphs, Levi abandons all pretense of classification and merely lists the 11 families that have classically been recognized.

The discussions of the families are frequently out of date (evidently the work was in press for an unusually long time) but contain numerous errors that cannot be attributed merely to age. For example, consider just the first half dozen families Levi discusses. (1) Liphistiids are characterized as having five pairs of heart ostia, but it was the discovery that *Heptathela sinensis* has only four pairs that led Petrunkevitch to establish the family Heptathelidae; the fact that at least one other species of *Heptathela* has retained all five pairs is insufficient reason to dismiss Petrunkevitch's observation. (2) *Liphistius* is said to occur "from Burma to the Moluccas" but in the entire Malay archipelago the genus is known from only one island, Sumatra. (3) There are said to be a dozen species of mecicobothriids in three genera (*Hexura*, *Microhexura*, and *Mecicobothrium*); at a time before *Microhexura* was shown to be a diplurid rather than a mecicobothriid, there would only

have been five described species in those three genera (even today, there are only eight known species in four genera). (4) Similarly, *Microhexura* has only four spinnerets, making Levi's characterization of the Mecicobothriidae as having six spinnerets false both at the time it was written and today (*Hexura rothi* also has only four spinnerets). (5) The atypids are said to have the sternum and labium fused, but that is true only for *Atypus* and *Sphodros*, not *Calommata*. (6) A lowly planarian (*Dugesia*) is promoted to the Theraphosidae. (7) The pycnothelids are said to be placed in two genera; even Schiapelli and de Pikelin's outdated 1965 revision of the family included four genera. (8) The pycnothelids are also said to have two pairs of spinnerets, even though *Diplothelopsis* has only a single pair.

Such errors are by no means restricted to these families. Particularly strange is the claim that there are only three genera of palpimanids (there are four genera in America alone, and the bulk of the group is African), and similarly incomplete lists of genera are given for the Tetrablemmidae and Ochyroceratidae. Since the Scytodidae, Loxoscelidae, and Sicariidae are each said to be monogeneric, one must conclude that *Drymusa* belongs to no family. We are told, incredibly, that pholcids are absent from Australia, and that leptonetids have two pairs of book lungs! In some cases, of course, it is possible that Levi's original text has been edited into nonsense (the Pholcoidea, for example, are said to have "one pair of spiracles, one which is posterior," whatever that means), and certainly the proofreading was inadequate (a list of spider sensory structures omits tarsal organs but includes "split sense organs," catering, one imagines, to the schizophrenic). But whatever the reasons for the mistakes, anyone using this compilation should obviously double-check both the classification and the character information against more reliable sources.

It may be that the most beneficial effect Levi's contribution will have is to convince arachnologists that no single worker can present a classification of all spiders, at this level of detail, without making major blunders. Perhaps the next general classification to be offered can be a collaborative effort, on the part of several systematists, that will not show the lack of first-hand knowledge of so many taxa that this work evidences.

I am grateful to my colleagues Val Davies, Charles Dondale, Ray Forster, Oscar Francke, Willis Gertsch, B. J. Kaston, Robert Raven, and Bill Shear for their comments and suggestions on a draft of this review, and for showing me that the details chosen for commentary here are just a sample drawn from a very extensive pool of possibilities.

Norman I. Platnick, Department of Entomology, American Museum of Natural History, New York, New York 10024.

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Grants-in-Aid for research on Arachnida (excluding Acarina) and Myriapoda are made available to students and researchers through the "*Exline-Frizzell Fund for Arachnological Research*" of the California Academy of Sciences. Applications, which will be evaluated by the American Arachnological Society and the Department of Entomology, California Academy of Sciences (Golden Gate Park, San Francisco, California 94118-9961, phone [415] 221-5100), may be submitted to the latter at any time. Application forms may be obtained upon request. Awards will be made upon the approval of the Academy's Director shortly after March 1 and September 1 yearly. Grants will normally not exceed \$750. The *Exline-Frizzell Fund* may be used for fieldwork, museum research (including travel), expendable supplies, and costs of publications (including artwork).

THE JOURNAL OF ARACHNOLOGY

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Figs. 27-34.—Right chelicerae of species of *A-us* from Timbuktu: Figs. 27, 29, 31, 33.—Dorsal views; Figs. 28, 30, 32, 34.—Prolateral views of movable finger; Figs. 27-28: *A-us x-us*, holotype male; Figs. 29-30: *A-us w-us* male; Figs. 31-32: *A-us z-us*, holotype male; Figs. 33-34: *A-us t-us*, male. Scale = 1.0 mm.

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