Journal of the New York Entomological Society

published by
The New York Entomological Society

Contents Volume 94, 1986, Numbers 1–4

Number 1

Book Review

Number 2

Contributions on Heteroptera in honor of Richard C. Froeschner

Foreword

Enicocephalomorpha

Nepomorpha

Cimicomorpha

Pentatomomorpha

Book Reviews

Number 3

Number 4

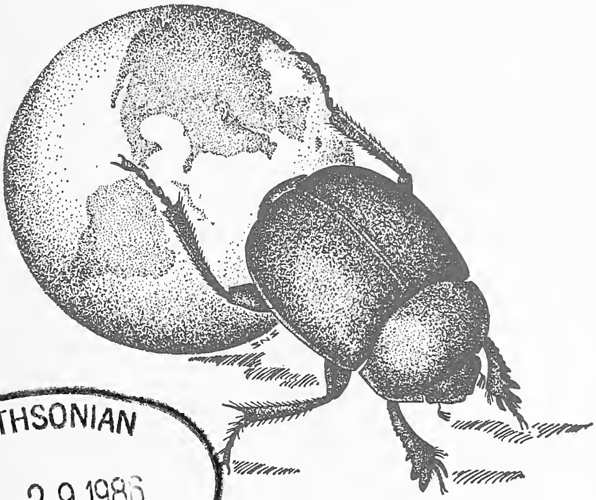
Vol. 94 JANUARY 1986 No. 1

Journal

of the

New York Entomological Society

(ISSN 0028-7199)



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Mailed January 16, 1986

The Journal of the New York Entomological Society (ISSN 0028-7199) is published quarterly (January, April, July, October) for the Society by Allen Press, Inc., 1041 New Hampshire, Lawrence, Kansas 66044. Second class postage paid at New Brunswick, New Jersey and at additional mailing office.

Known office of publication: American Museum of Natural History, New York, New York 10024.

Journal of the New York Entomological Society, total copies printed 850, paid circulation 700, mail subscription 700, free distribution by mail 18, total distribution 718, 132 copies left over each quarter.

J. New York Entomol. Soc. 94(1):1–15, 1986

REVISION OF *COSMOPEPLA* STÅL (HEMIPTERA: PENTATOMIDAE)

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Abstract.—The Western Hemisphere species of *Cosmopepla* Stål are revised and a key provided for identification. *Eysarcoris intergressus* Uhler is transferred to this genus. *C. humboldtensis* Bliven is a junior synonym of *C. intergressa* (Uhler).

Cosmopepla Stål, 1867 is a genus of small pentatomids, generally black with red or yellow markings or speckled brown which are distributed widely over Canada, U.S.A., to a lesser extent Mexico, and with only one species recorded from South America. The genus *Eysarcoris* Hahn, 1834 has been confused with *Cosmopepla* and two species in America have been wrongly assigned to that genus. Examination of the holotype of *Eysarcoris alienus* Walker shows that this is an *Edessa* sp. and *E. intergressus* is transferred to *Cosmopepla.* Little is known of the biology of *Cosmopepla* species except for *C. lintneriana* (Kirkaldy) which has a great deal of literature on its life cycle and host preferences (McPherson, 1982).

From an examination of the genitalia, *Cosmopepla* would appear to be related to the holarctic genera *Holcostethus* Fieber, *Trichopepla* Stål and *Codophila* Mulsant by virtue of the genital plates on the margin of the pygophore. However in *Cosmopepla* these are plate-like whereas in the other genera they are much more like appendages and have been termed pseudoclaspers (McDonald, 1974, 1976). *Cosmopepla,* like *Codophila* and *Trichopepla,* possesses no median penial lobes; *Holcostethus* has well developed median penial lobes. *Cosmopepla* has a typically pentatomid type spermatheca with no spines on the bulb of the pump similar to *Codophila*; *Holcostethus* is similar but possesses spines on the spermathecal bulb (McDonald, 1974). *Trichopepla* on the other hand has a very simple primative type spermatheca (McDonald, 1976). The only other genus with genital plates, *Dendrocoris* (McDonald, 1966), is generally placed in group II of the Pentatomini (Rolston and McDonald, 1981). It bears some resemblance to *Cosmopepla* but is not, I believe, closely related. There is no doubt that by virute of their geographic distribution and similarities in the male and female genitalia that *Cosmopepla, Codophila, Holcostethus* and *Trichopepla* are related, with *Cosmopepla* being more distantly related to the other three genera.

Cosmopepla Stål

Cosmopepla Stål, 1867, p. 525, 1872, p. 18; Distant, 1880, p. 52; Provancher, 1885, p. 44; Montandon, 1893, p. 45; Van Duzee, 1904, p. 50; Kirkaldy, 1909, p. 80; Zimmer, 1912, p. 22; Van Duzee, 1917, p. 49; Stoner, 1920, pp. 61, 96–97; Blatchley, 1926, pp. 151–152.

Type species. Cosmopepla carnifex = lintneriana.

Description. Small species never more than 8 mm long and 5 mm wide (across pronotum); black or bluish black with orange or yellow markings, or speckled brown or brown-red. Head with juga and tylus equal or subequal. Antennae slender, pubescent, length of segments variable, fifth always longest. Rostrum reaching or just surpassing base of metasternum. Pronotum with anterior portion declivent, margins without spines or serrations. Scutellum broad, apex broadly rounded lying behind apices of coria. Ostiolar opening raised on a small mound with an auriculate sulcus; evaporative area variable. Legs, tibiae not sulcate, densely pubescent, remaining segments with some pubescence.

Male genitalia: Pygophore provided with genital plates on dorsal margin; ventral margin with a shallow depression below it, centrally excavated or notched. Claspers broad, spatulate with a small thumb-like process except in *C. decorata* and *C. conspicillaris.* Two conjunctival appendages, a large dorsal pair and a much smaller ventral pair. Median penial lobes not developed. Ejaculatory duct moderately long S-shaped, reservoir small, globose.

Female genitalia: External genitalia typically pentatomoid. Only in *C. decorata* and *C. conspicillaris,* are the 2nd gonocoxae visible externally. Spermatheca typically pentatomoid, dilation well developed with internal rod, basally curved. Pump with well developed proximal and distal flanges, bulb ovoid-elongate.

KEY TO SPECIES OF *Cosmopepla*

1. Species black or metallic blue-black with markings in red, yellow or orange 3
– Species overall speckled brown or reddish brown with markings in orange or black ... 2
2. Reddish brown species with a distinct irregular transverse orange band across center of pronotum .... *C. ulheri* Montandon
– Reddish brown or speckled brown species without orange band on pronotum .... *C. intergressa* (Uhler)
3. Scutellum with two distinct marginal red spots, one on each side near apex .... *C. bimaculata* (Thomas)
– Scutellum without spots, apex may be margined in yellow or orange 4
4. Pronotum with a transverse yellow stripe bisected centrally by a perpendicular stripe forming a distinct cross on disc (Fig. 45) .... *C. cruciaria* Stål
– Pronotal markings otherwise 5
5. Pronotum with a transverse yellow band expanded medianly and bearing two small black maculae close together (Fig. 44) .... *C. binotata* Distant
– Pronotal band uniform or irregular with maculae widely spaced 6
6. Pronotal band across disc irregular, orange or red, bearing two large maculae well separated (Fig. 43) .... *C. conspicillaris* (Dallas)
– Pronotal band uniformly narrow 7
7. Frenum not quite ⅓ length of the scutellum; shape of body broadly oval. Male clasper with a distinct apical thumb-like process (Fig. 36). Female with 1st gonocoxae triangular in outline (Fig. 26) .... *C. coeruleata* Montandon
– Frenum reaching almost ½ length of scutellum; body generally longer and more tapering. Male clasper without apical process (Fig. 2). Female with 1st gonocoxae oblong in outline (Fig. 6) .... *C. decorata* Hahn

Note. In the following descriptions mean measurements are given, followed by a range and the number of specimens on which each measurement is based. Length of each specimen is measured from the apex of the tylus to base of abdomen, the width is taken across the pronotal angles.

Cosmopepla decorata (Hahn)

Figs. 1–7

Eysarcoris decoratus Hahn, 1834, p. 117; Dallas, 1851, p. 225.

Pentatoma decorata Herrich-Schaeffer, 1853, p. 96.

Cosmopepla decorata Stål, 1872, p. 19; Uhler, 1876, p. 284, 1886, p. 5; Distant, 1887, p. 60; Montandon, 1893, pp. 46–47; Uhler, 1894, p. 228; Van Duzee, 1904, p. 52; Barber, 1906, p. 259; Kirkaldy, 1909, p. 80; Van Duzee, 1917, p. 50.

Type. Not located.

Description. Head black. Antennae and rostrum piceous. Pronotum with anterolateral margins yellow, a narrow yellow band, extending across the disc between lateral angles, remainder of prothorax shiny black. Scutellum black, apex with a crescent shaped yellow macula. Hemelytra black, apical ⅓ of corial margin yellow. Sterna and pleura black. Legs piceous. Abdomen with connexiva yellow. Sterna shiny black with broad yellow band around outer margins extending onto metapleura. Males, pygophore black. Females, 8th and 9th paratergites yellow. 1st gonocoxae divided diagonally into apical black and basal yellow sections.

Male genitalia: Pygophore. Ventral margin with a distinct inferior ridge centrally notched. Genital plates large triangular. Claspers spatulate without thumb-like process. Aedeagus. Theca cylindrical with two small processes one on each side near base. Two pairs of membranous conjunctival appendages, dorsalmost large, cylindrical, apically sclerotized. Ventral conjunctival appendages smaller, lying centrally. Ejaculatory duct S-shaped.

Female genitalia: 8th paratergites triangular, 9th oblong. 1st gonocoxae somewhat rectangular. 2nd gonocoxae, small oblong structures lying below 1st gonocoxae. Spermatheca with well developed elongate reservoir; spermathecal pump ovoid with well developed proximal and distal flanges.

Distribution. U.S.A.: Arizona, Texas, California, New Mexico. MEXICO: Veracruz, Baja California, Mexico D.F., Jalisco. VENEZUELA: Merida. EL SALVADOR: San Salvador.

Comments. (1) The yellow markings on the prothorax scutellum, and hemelytra can vary from pale yellow to bright orange-red.

(2) This species resembles closely *C. coeruleata* Montandon (1893). In his paper Montandon (1893) gave a series of characters to separate the two species. The males can readily be separated by the fact that the claspers in *C. coruleata* have a distinct apical thumb-like process, absent in *C. decorata.* In the females, the 1st gonocoxae in *C. decorata* are distinctly oblong (Fig. 6), whereas, in *C. coeruleata* they are more triangular shaped.

(3) This species is common on mints (*Labiatae*) especially the common horehound *Marrhubium vulgare* in Mexico.

Measurements. Female. Length 6.34, range 5.52–6.96 (25); breadth 4.24, range 3.76–4.72 (25). Male. Length 5.95, range 5.20–6.88 (25); breadth 4.10, range 3.68–4.48 (25).

Cosmopepla conspicillaris (Dallas)

Figs. 8–14, 43

Eysarcoris conspicillaris Dallas, 1851, p. 225.

Pentatoma conspicillaris Herrich-Schaeffer, 1853, p. 153.

Cosmopepla conspicillaris Stål, 1872, p. 19; Uhler, 1875, p. 830, 1876, p. 284; Distant, 1880, p. 53; Montandon, 1893, pp. 46, 49; Uhler, 1894, p. 229; Gillette and Baker, 1895, p. 14; Van Duzee, 1904, p. 51; Kirkaldy, 1909, p. 80; Banks, 1910, p. 84; Van Duzee, 1917, pp. 49–50; Stoner, 1920, p. 13; Baker, 1931, pp. 198–199.

Holotype. ♀, California. British Museum (Natural History) (Hem. 1103). Type seen by author.

Description. Head black. Antennae and rostrum piceous. Pronotum black with anterior and lateral margins outlined in yellow. Central vertical yellow stripe running from anterior margin almost to posterior margin. Across center of disc running between lateral angles is a jagged orange band containing two black maculae, one on either side of the central vertical yellow stripe (Fig. 43). Scutellum black, apex margined in yellow. Corium, clavus piceous, upper half of corial margin outlined in yellow. Sterna, pleura black. Legs piceous. Abdomen with sterna black, outer margins with irregular crenate yellow band extending on each side onto the metapleuron.

Male genitalia: Pygophore similar to *C. decorata,* genital plates crescent shaped. Claspers with square apex. Aedeagus with dorsal conjunctival appendages with broadly rounded apices, moderately sclerotized.

Female genitalia: Similar to *C. decorata.*

Distribution. U.S.A.: Idaho, Colorado, Utah, Montana, California, Oregon, Washington. CANADA: Vancouver Is., British Columbia. MEXICO: Baja California.

Comment. Downes (1928) states that this species is common on flowers of *Stachys palustris.*

Measurements. Female. Length 6.59, range 5.76–7.84 (25); breadth 4.13, range 3.28–4.88 (25). Male. Length 6.09, range 5.40–6.80 (25); breadth 3.90, range 3.50–4.40 (25).

Cosmopepla lintneriana (Kirkaldy)

Fig. 15

Cimex carnifex Fabricius, 1798, p. 535 (name preoccupied by *C. carnifex* = *Lygaeus carnifex* Fabricius, 1775); Coquebert, 1801, p. 81; Fabricius, 1803, p. 117.

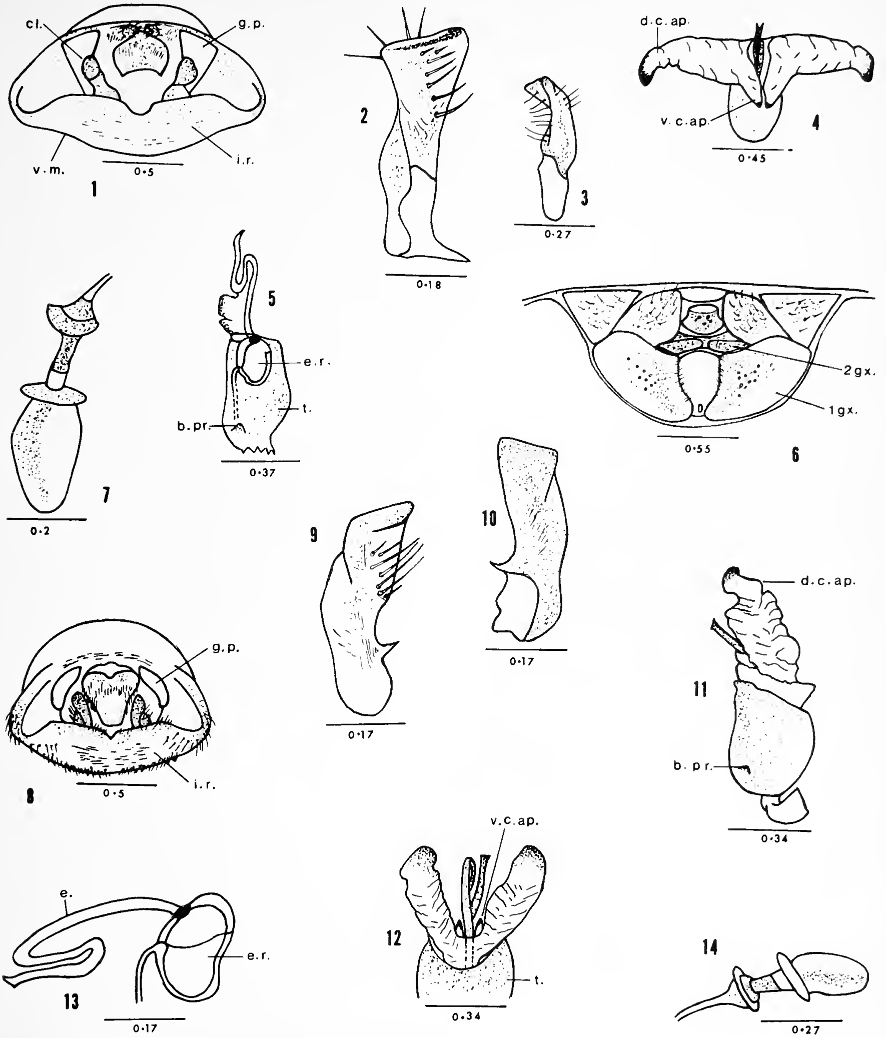
Eysacoris carnifex Hahn, 1834, p. 117; Dallas, 1851, p. 225.

Pentatoma carnifex Kirby, 1837, p. 275; Herrich-Schaeffer, 1853, p. 153.

Pentatoma bimaculata Thomas, 1865, p. 45 (name preoccupied by *P. bimaculata* Westwood, 1837).

Cosmopepla carnifex Stål, 1867, p. 525, 1868, p. 28, 1872, p. 18; Uhler, 1872, p. 395, 1876, p. 284, 1877, p. 403, 1878(a), p. 376, 1878(b), p. 504; Provancher, 1885, p. 44; Uhler, 1886, p. 5; Lintner, 1886, pp. 144–148; Van Duzee, 1889, p. 2; Montandon, 1893, p. 46; Van Duzee, 1894, p. 170; Howard, 1898, pp. 100–101; Lugger, 1900, p. 91; Van Duzee, 1904, pp. 50–51, 1908, p. 109; Olsen, 1912, p. 54.

Cosmopepla bimaculata Van Duzee, 1917, p. 49; Stoner, 1920, pp. 96–97, 1926, p. 29; Blatchley, 1926, pp. 152–153; Leonard, 1928, p. 82 (localities); Baker, 1931,



Figs. 1–14. 1–7.—*Cosmopepla decorata.* 1. Pygophore, caudal. 2. Right clasper, ectal. 3. Right clasper, lateral. 4. Aedeagus, ventral. 5, Aedeagus, lateral (conjunctival appendages omitted). 6. Female genital plates, ventral. 7. Spermatheca. 8–14.—*Cosmopepla conspicillaris.* 8. Pygophore, caudal. 9. Right clasper, ectal. 10. Right clasper, ental. 11. Aedeagus, lateral. 12. Aedeagus, dorsal. 13. Ejaculatory reservoir. 14. Spermatheca. b.pr., basal process; cl., clasper; d.c.ap., dorsal conjunctival appendage; e., ejaculatory duct; e.r. ejaculatory reservoir; g.p., genital plate; 1 gx., 1st gonocoxa; 2 gx., 2nd gonocoxa; i.r., inferior ridge; t., theca; v.c. ap., ventral conjunctival appendage; v.m. ventral margin.

pp. 102–106; McDonald, 1966, pp. 25, 51 (male and female genitalia); McPherson, 1982, pp. 73–74 (complete listing of biological records).

Cosmopepla lintneriana Kirkaldy, 1909, p. 80.

Note. In 1865 the name *Pentatoma bimaculata* Thomas was preoccupied by *P. bimaculata* Westwood, 1837, p. 35. This latter species was transferred to *Carbula insocia* (Walker) by Distant, 1900, p. 812.

Holotype. C. carnifex, ♀, America, Dom Hybner. Universitets Zoologiske Museum, Copenhagen. Type seen by author.

Description. Described by Blatchley, 1926.

Male genitalia: Described by McDonald (1966) and Baker (1931).

Female genitalia: Described by McDonald (1966).

Distribution. Throughout U.S.A. and Canada, Mexico.

Measurements. Female. Length 5.93, range 5.20–6.50 (25); breadth, 3.98, range 3.51–4.42 (25). Male. Length 5.38, range 4.74–6.04 (25); breadth 3.72, range 3.51–4.16 (25).

Cosmopepla cruciaria Stål

Figs. 16–20, 45

Cosmopepla cruciaria Stål, 1872, p. 19; Montandon, 1893, pp. 46–47; Kirkaldy, 1909, p. 80.

Holotype. ♀, Bogota, lindiq. Naturhistoriska Riksmuseet, Stockholm. Type seen by author.

Description. Head black, juga apically yellow. Antennae with rostrum piceous. Pronotum with anterior margin yellow, anterolateral margins with broad yellow stripe continuing across disc between lateral angles. A vertical yellow stripe extending between anterior and posterior margins centrally, forming a broad cross (Fig. 45); remainder of pronotum black. Scutellum black, margins yellow extending into broad yellow macula at apex. Hemelytra black, apical ⅓ of corial margin yellow. Sterna, pleura black. Legs dark brown. Abdomen with connexiva yellow. Sterna black with a broad yellow band around outer margins, extending onto metapleura. Male with pygophore piceous. Female with 8th and 9th paratergites yellow, 1st gonocoxae yellow, apex brown.

Male genitalia: Very similar to *C. decorata.* Genital plates somewhat crescent shaped. Clasper with thumb-like process somewhat more acute.

Female genitalia: Similar to *C. decorata.*

Distribution. Colombia. Ecuador.

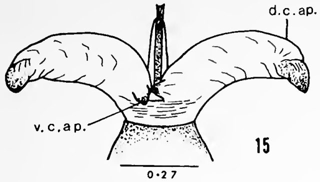
Comment. In some specimens the jugae are entirely black.

Measurements. Female. Length 5.38, range 4.96–6.48 (10); breadth 4.20, range 3.60–4.72 (10). Male. Length 5.46, range 5.20–5.76 (10); breadth 4.04, range 4.00–4.16 (4).

Cosmopepla binotata Distant

Figs. 21–27, 44

Cosmopepla binotata Distant, 1889, p. 327, pl. 31; Montandon, 1893, pp. 46, 49; Van Duzee, 1904, p. 51; Kirkaldy, 1909, p. 80; Banks, 1910, p. 83; Barber, 1910, p. 35; Van Duzee, 1917, p. 50.



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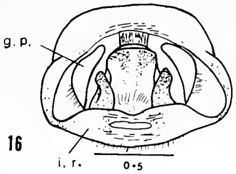

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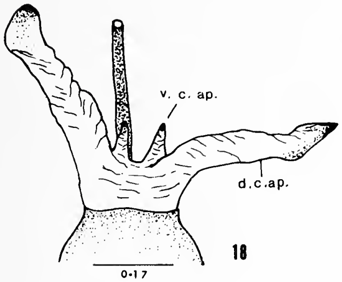

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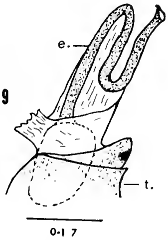

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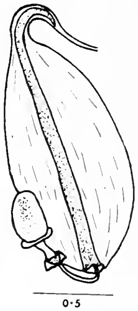

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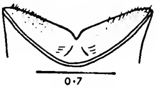

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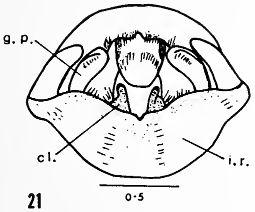

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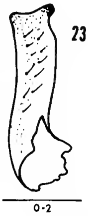

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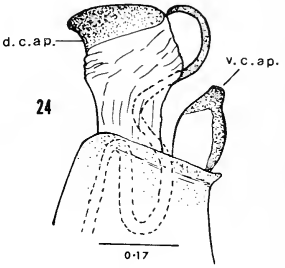

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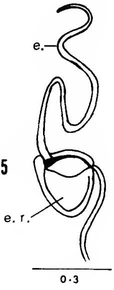

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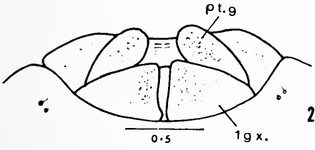

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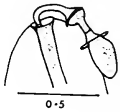


27

Figs. 15–27. 15.—*Cosmopepla bimaculata.* Aedeagus, ventral. 16–20.—*Cosmopepla cruciaria.* 16. Pygophore, caudal. 17. Right clasper, ectal. 18. Aedeagus, dorsal. 19. Aedeagus, lateral (conjunctival appendages omitted). 20. Spermatheca. 21–27.—*Cosmopepla binotata.* 21. Pygophore, caudal. 22. Pygophore, ventral margin. 23. Right clasper, ectal. 24. Aedeagus, lateral. 25. Ejaculatory reservoir. 26. Female genital plates, ventral. 27. Spermatheca. cl., clasper; d.c.ap., dorsal conjunctival appendage; e., ejaculatory duct; e.r., ejaculatory reservoir; g.p., genital plate; i.r., inferior ridge; pt.9, paratergite 9; t., theca; v.c.ap., ventral conjunctival appendage.

Holotype. ♀, Ciudad Mexico, 8,100 ft. Forrer. British Museum (Natural History) (HEM. 1104). Type seen by author.

Description. Head black. Anterior lobes of bucculae tipped with yellow. Antennae and rostrum piceous. Pronotum black, anterolateral margins outlined in orange; broad yellow band running between lateral angles and across center of disc; in center of band, pair of small black spots (Fig. 44). Scutellum black, apex orange. Corium, clavus black with basal half of corial margins outlined in orange. Sterna and pleura black except for oval yellow maculae on episterna adjacent to coxal margin. Legs piceous. Abdomen with connexiva black with outer margin outlined in yellow. Sterna black with broad yellow band extending around outer margins and onto metapleura. Spiracle and trichobothria surrounded by black spherical macula on each segment.

Male genitalia: Pygophore, ventral margin with well developed inferior ridge sitting vertically above margin with deep median notch. Pygophoral plates oval in outline. Clasper with small thumb-like process, somewhat sinuous in outline viewed ectally. Aedeagus similar to *C. decorata,* dorsal conjunctival appendages broadly rounded and sclerotized at their apices. Ventral conjunctival appendages larger, lobe-like, bluntly rounded; sclerotized at apex and along outer margin. Ejaculatory duct much more broadly S-shaped.

Female genitalia: 9th paratergites oblong. First gonocoxae large, triangular, completely covering very narrow second gonocoxae. Spermatheca similar to *C. decorata.*

Distribution. U.S.A.: Arizona, New Mexico, Utah. MEXICO: Chihuahua, Mexico State, Durango, Nuevo Leon.

Comment. Ruckes (1938) reported this species on *Penstemon fendlesi.*

Measurements. Female. Length 6.38, range 5.60–6.72 (15); breadth 4.10, range 3.60–4.48 (15). Male. Length 5.66, range 5.12–5.84 (6); breadth 4.01, range 3.92–4.16 (6).

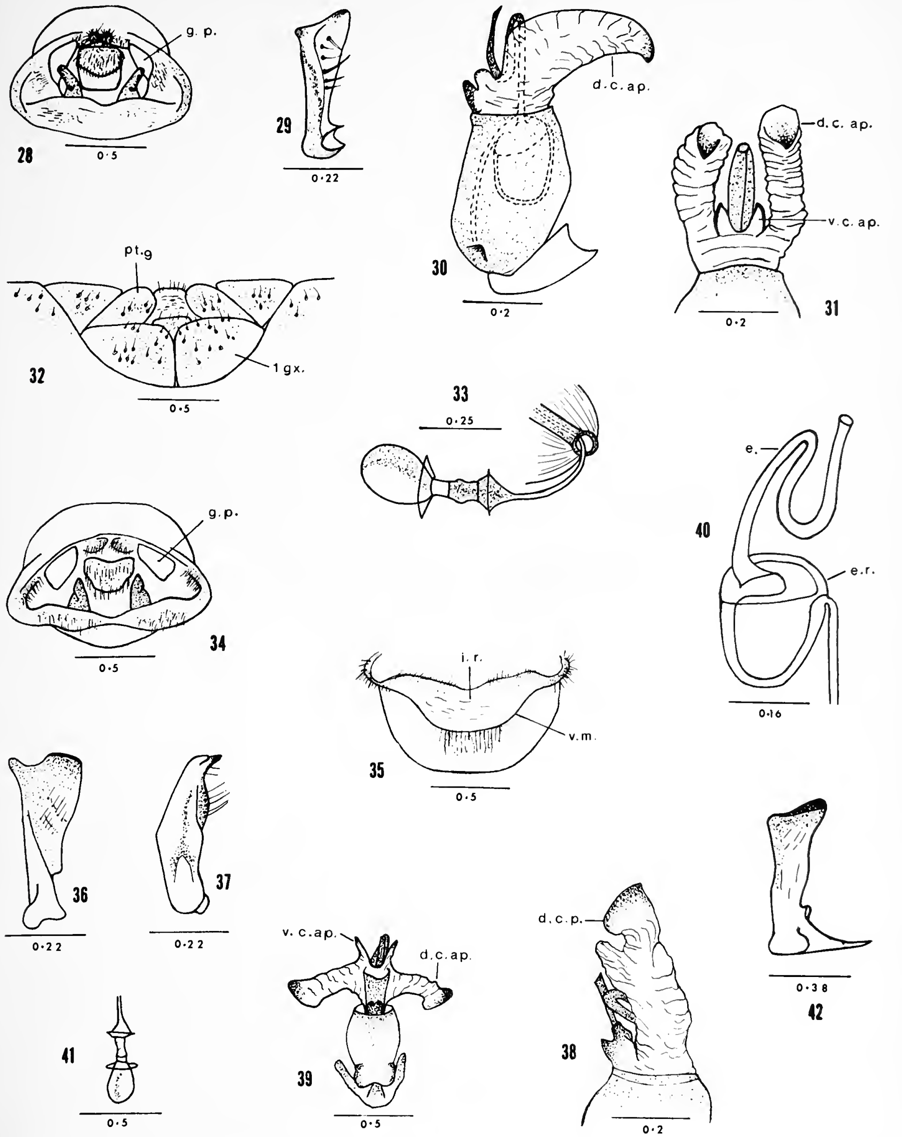
Cosmopepla uhleri Montandon, 1893
Figs. 28–33, 46

Cosmopepla uhleri Montandon, 1893, pp. 46, 48; Van Duzee, 1904, p. 51; Snow, 1906, p. 177; Kirkaldy, 1909, p. 80; Banks, 1910, p. 84; Van Duzee, 1914, p. 4, 1917, p. 49.

Type. Not located.

Description. Head black. Antennae dark brown. Rostrum and segments 1–3 mid-brown, segment 4 black.

Pronotum with basal half rust brown, apical half with two oblong black maculae extending from anterior margin towards center of disc. Anterolateral margins outlined with orange. A broad irregular orange band extending from lateral angles across disc (Fig. 46). Scutellum, basal ⅓ black, apical ⅔ rusty brown. Hemelytra, corium, clavus rusty brown, membrane black and sterna piceous, except for oblong ivory maculae on epimera and episterna adjacent to coxal bases. Orange anterolateral pronotal margins, centrally extended as triangular orange patch on propleuron. Legs dark to reddish brown. Abdomen with connexiva alternated yellow and black. Sterna black with a broad crenate yellow band around outer margins. Small oblong black maculae found at segmental junctions along outer margin of sterna.



Figs. 28–42. 28–33.—*Cosmopepla uhleri.* 28. Pygophore, caudal. 29. Right clasper, ectal. 30. Aedeagus, lateral. 31. Aedeagus, dorsal. 32. Female genital plates, ventral. 33. Spermatheca. 34–41.—*Cosmopepla coeruleata.* 34. Pygophore, caudal. 35. Pygophore, ventral margin. 36. Right clasper, ectal. 37. Right clasper, lateral. 38. Aedeagus, lateral. 39. Aedeagus, ventral. 40. Ejaculatory reservoir. 41. Spermathecal bulb. 42.—*Cosmopepla intergressa.* Right clasper, ectal. d.c.ap., dorsal conjunctival appendage; e., ejaculatory duct; e.r., ejaculatory reservoir; g.p., genital plate; i.r., inferior ridge; v.c.ap., ventral conjunctival appendage; v.m., ventral margin.

Male genitalia: Similar to *C. decorata.*

Female genitalia: Similar to *C. decorata.*

Distribution. U.S.A.: California, Oregon, Nebraska, Utah, Arizona, Nevada, Washington, Idaho.

Comments. (1) The orange band across the disc of the pronotum and around the margins of the abdominal sterna can vary from red to yellowish brown.

(2) There is very little that distinguishes this species from *C. intergressa* except the distinctive coloration. The genitalia are exactly the same, however the rostrum is significantly longer in *C. intergressa* on the average. The two species extend throughout most of the same geographic range and the biology of each would have to be studied in order to determine the exact status of these species. I have retained *C. uhleri* as a good species as it can be readily separated by the broad orange band across the center of the pronotal disc from *C. intergressa.* This species has been taken on *Aquilegia* sp.

Measurements. Female. Length 5.28, range 4.80–6.00 (25); breadth 3.57, range 3.04–4.00 (25). Male. Length 4.73, range 4.16–5.36 (17); breadth 3.26, range 2.96–3.76 (17).

Cosmopepla coeruleata Montandon

Figs. 34–41

Cosmopepla coeruleata Montandon, 1893, pp. 46–47; Kirkaldy, 1909, p. 80.

Syntype. ♀, Costa Rica, H. Donckier. Institute Royal des Sciences Naturelles de Belgique, Brussels. Syntype seen by author.

Description. Head blue black. Antennae dark brown, segments 2 and 3 equal, 5 longest. Rostrum dark brown extending just beyond hind coxae. Pronotum with anterolateral margins yellow; a narrow yellow band extending between pronotal angles across center of disc. Scutellum black with metallic blue sheen, apical margin with a yellow crescent-shaped macula. Apical half of corial margin yellow, remainder together with clavus metallic blue-black. Pleura, sterna black with metallic blue sheen. Legs dark brown. Abdomen with connexiva yellow. Sterna black, with a broad yellow band extending around outer margins and onto metapleura.

Male genitalia: Pygophore similar to *C. bimaculata.* Claspers with rather more prominent thumb-like process apically. Aedeagus similar to *C. bimaculata,* apex of dorsal conjunctival appendages somewhat more bluntly rounded.

Female genitalia: Similar to *C. bimaculata,* spermathecal bulb more rounded.

Distribution. U.S.A.: Texas. MEXICO: Jalisco. EL SALVADOR: San Salvador. COSTA RICA. VENEZUELA: Merida. COLOMBIA: Cundinamarca.

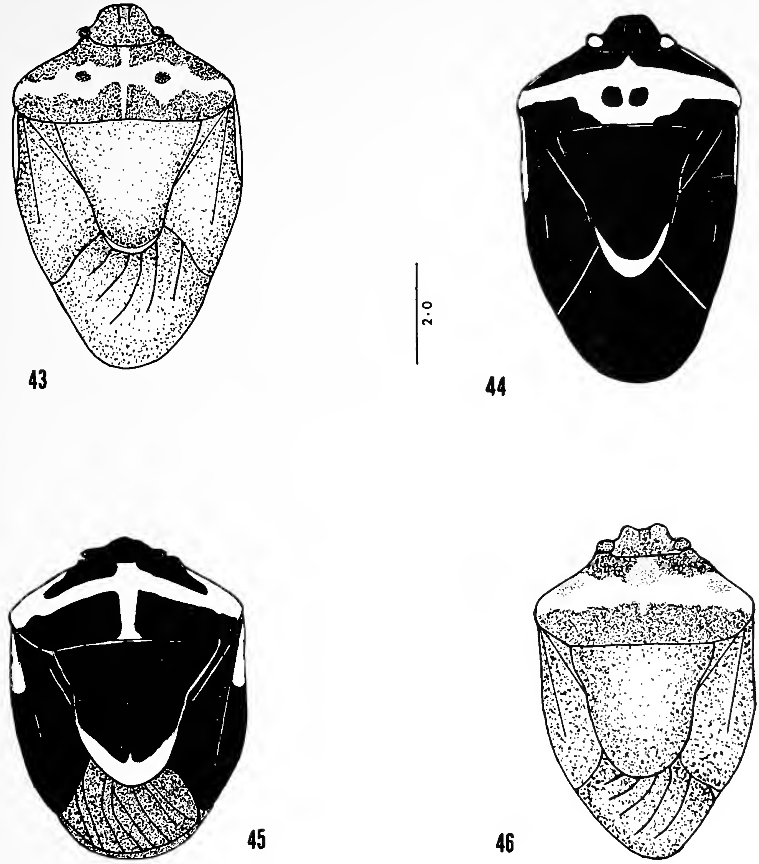
Measurements. Female. Length 5.85, range 5.44–6.40 (13); breadth 4.00, range 3.52–4.56 (13). Male. Length 5.35, range 5.12–5.68 (15); breadth 3.76, range 3.44–4.08 (15).

Cosmopepla intergressa (Uhler), **New Combination**

Fig. 42

Eysarcoris melanocephalus Uhler, 1876.

Eysarcoris intergressus Uhler, 1893, p. 368; Van Duzee, 1904, p. 52; Kirkaldy, 1909,



Figs. 43–46. 43. *Cosmopepla conspicillaris.* Fig. 44. *C. binotata.* Fig. 45. *C. cruciaria.* Fig. 46. *C. uhleri.*

p. 85; Van Duzee, 1917, p. 50; McDonald, 1966, pp. 24–25, 51 (male and female genitalia).

Neottiglossa intergressa Gillette and Baker, 1895, p. 14.

Cosmopepla humboldtensis Bliven, 1955, p. 8, 1956, pp. 5, 23. **New Synonymy.**

Lectotype. ♂, Cal. United States National Museum, Washington. Lectotype seen by author. The holotype ♂ of *C. humboldtensis,* California Academy of Sciences, San Francisco has also been seen.

Description. Small speckled brown species. Head black with juga reddish brown and reddish brown stripe along center. Bucculae reddish brown. Antennae light brown. Rostral segments 1–3 light brown, 4 dark brown. Pronotum with two large square black maculae one in each anterolateral corner, remainder of pronotum pale coffee-brown overlaid with dark brown punctations. Scutellum with 3 ivory spots along posterior margin, one centrally and one in each lateral angle. Remainder of scutellum pale coffee-brown suffused with black towards posterior margin and overlaid by brown punctations. Propleura, apical half black, basal half orange brown; mesopleura black except for a square area adjacent to the mesocoxae, pale brown. Evaporative area of stink gland finely granular, extending onto mesopleuron; metapleural section with inner half finely granular and light brown, outer half black with coarse punctations. Basal half of metapleuron ivory overlaid with dark punctations. Legs amber, femora with suffused patches of dark brown; tibiae with fine brown punctations. Abdomen with connexiva alternating tan brown and dark brown. Sterna black with a wide crenate margin of ivory overlaid with dark punctations; small dark brown maculae at lateral junctions of each segment. Small brown maculae found in the marginal band, centrally on segments 3, 4, 5 and 6.

Male genitalia: See McDonald (1966).

Female genitalia: See McDonald (1966).

Distribution. U.S.A.: Kansas, Colorado, Utah, Montana, Idaho, Nevada, Missouri, California, Oregon, Washington. CANADA: Vancouver Is., British Columbia.

Comment. (1) Some specimens are a distinct red-brown color, with an orange-brown band around the margin of the abdominal sterna.

(2) Pack and Knowlton (1930) report this species is found on "currants," Downes (1928) records them on *Rubus parviflorus.* They can also be found abundantly on *Ribes* sp.

Measurements. Female. Length 5.24, range 4.64–6.08 (25); breadth 3.61, range 3.28–4.08 (25). Male. Length 4.69, range 4.16–5.44 (25); breadth 3.33, range 2.96–3.68 (25).

ACKNOWLEDGMENTS

I wish to thank the following for the loan of type and other material. Dr. N. Møller Andersen, Universitets Zoologiske Museum, Copenhagen; Mr. W. R. Dolling, British Museum (Natural History), London; Dr. Per Lindskog, Naturhistoriska Riksmuseet, Stockholm; Dr. P. Dessart, Institute Royal des Sciences de Belgique, Brussels; Dr. Paul H. Arnaud Jr., California Academy of Sciences, San Francisco; Dr. Randall T. Schuh, American Museum of Natural History, New York; Dr. Richard C. Froeschner, National Museum of Natural History, Washington.

I should also like to thank Professor L. H. Rolston, Department of Entomology, Louisiana State University, Baton Rouge for the original literature survey and helpful comments during the progress of this research.

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Received December 6, 1984; accepted July 8, 1985.

J. New York Entomol. Soc. 94(1):16–19, 1986

NEW ONCIDERINI FROM SANTA ROSA NATIONAL PARK, COSTA RICA (COLEOPTERA: CERAMBYCIDAE)

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Abstract.—*Oncideres santarosae* and *Lochmaeocles tessellatus costaricae* are described as new from Costa Rica. Known hosts are listed and a dorsal view figure of *O. santarosae* is provided.

A collection of Cerambycidae from Santa Rosa National Park, Costa Rica was made available for study by D. H. Janzen. Among the material were two undescribed girdlers of the tribe Onciderini. These are described below to make the names available for ecological studies.

Carolyn Tibbetts is gratefully acknowledged for preparing the illustration.

Oncideres santarosae, new species

Fig. 1

Description. Male: Form moderate sized, cylindrical, tapering posteriorly behind middle; integument reddish brown, head, pronotum, and antennae darker brown; pubescence fine, appressed, grayish and brown-orange. Head with front quadrate, bordered by longitudinal, slightly curved carinae, median carina shallow; punctures minute, dense; genae slightly shorter than lower eye lobe; pubescence thin on front, dense on vertex and sides, dense pubescence grayish and brownish intermixed, vertex usually with two longitudinal darker brown vittae; antennal tubercles strongly projecting forward and slightly inward; antennae slightly longer than body, scape short, globose, second and third segments thickened, remaining segments gradually becoming thinner, basal three segments dark brownish, remaining segments usually darker at apical one-half, basal segments moderately densely, rather coarsely pubescent, outer segments finely, densely clothed with short, pale, appressed pubescence, basal segments with a few, very short, black, suberect setae beneath. Pronotum broader than long, sides with a small acute tubercle behind middle; disk with a rounded glabrous callus behind middle, transverse rugosities present before median callus and behind shallow apical sulcus; small glabrous, seta-bearing punctures present around lateral tubercles, punctures obsolete elsewhere; pubescence dense, appressed, usually brownish apically and grayish basally; prosternum narrow, densely pale pubescent, coxae prominent, obtusely tuberculate internally near apex, intercoxal process arcuate; meso- and metasternum densely pale pubescent, mesosternal process abruptly declivous. Elytra about twice as long as broad; base obtusely gibbose on each side; large, glabrous asperites present behind basal margin, becoming smaller, sparser, and less elevated toward basal one-third; punctures behind middle smaller, glabrous, rather sparse, each bearing a short pale seta; pubescence short, appressed, brownish and grayish variegated, base with an indistinct transverse brownish fascia, middle

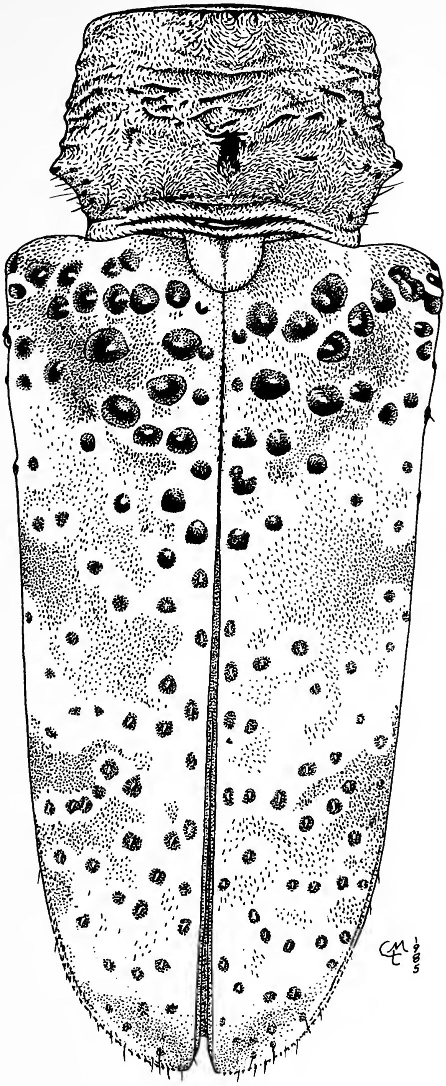

Fig. 1. Pronotum and elytra of *Oncideres santarosae* Chemsak, ♂.

with vague oblique fasciae not attaining suture, apical one-third with a transverse brownish fascia; apices rounded. Scutellum uniformly gray pubescent. Legs short, femora clavate, profemora rugose beneath; pubescence brownish and gray variegated, tibiae and tarsi usually darker. Abdomen uniformly grayish pubescent; last sternite emarginate at apex. Length, 18–20 mm.

Female: Form similar, more robust. Head with antennal tubercles not strongly projecting; antennae shorter than body, scape not robust, third segment not thickened, arcuate. Legs with femora less robust, profemora not rugose beneath. Abdomen with last sternite medially impressed. Length, 18–22 mm.

Type material. Holotype male, allotype (California Academy of Sciences) from Santa Rosa National Park, Guanacaste Prov., Costa Rica, June 17–19, 1980, July 16–18, 1980 (D. H. Janzen, W. Hallwachs). Paratypes (Essig Museum and D. H. Janzen), all from the type locality as follows: 2 males, 1 female, June 8–13, 1980 (Janzen and Hallwachs); 1 female, July 1–3, 1980 (Janzen and Hallwachs); 1 female 1980 (Janzen); 1 male, November 7–9, 1979 (Janzen); 2 females, 1979 (Janzen); 1 female, 1981 (Janzen).

Diagnosis. The combination of the prominently projecting antennal tubercles and thickened third antennal segment of males, the large, glabrous asperites and the transverse brownish fasciae of the elytra makes this species distinctive.

The coloration of the pubescence varies from brown-orange to dark brown and the sides of the mesosternum and an anterior patch on the metepisternum are frequently brownish.

D. H. Janzen (pers. comm.) reports that this species works high up in the trees of *Bursera simaruba* (L.) Sargent, cutting off large branches.

Lochmaeocles tessellatus costaricae, new subspecies

Description. Form and size of *L. tessellatus tessellatus* (Thomson). Elytra basally punctate, rarely with a few small, glabrous asperites; pubescence consisting of fewer orangish rounded patches near base and toward apex, patches rather uniform in size, smaller patches usually lacking; disk tending to be densely pubescent between orange patches. Scutellum usually brownish pubescent medially. Length 16–27 mm.

Type material. Holotype male, allotype (California Academy of Sciences) from Santa Rosa National Park, Guanacaste Prov., Costa Rica, December 21–24, 1979, July 1–3, 1979 (D. H. Janzen). Paratypes, all from the type locality as follows: 1 female, May 2–11, 1980 (Janzen and Hallwachs); 1 male, May 12–14, 1980 (Janzen and Hallwachs); 1 female, May 18–22, 1978 (Janzen); 1 male, May 26–28, 1980 (Janzen and Hallwachs); 1 male, June 9–14, 1978 (Janzen); 1 female, June 20–24, 1978 (Janzen); 2 females, June 27–30, 1979 (Janzen); 1 male, 1 female, July 1–3, 1979 (Janzen); 1 male, July 4–6, 1980 (Janzen and Hallwachs); 1 male, July 11–17, 1981 (Janzen and Hallwachs); 1 male, July 16–18, 1979 (Janzen); 1 male, July 19–21, 1979 (Janzen); 1 male, July 22–24, 1979 (Janzen); 1 male, July 25–27, 1979 (Janzen); 1 male, December 15–17, 1979 (Janzen); 1 male, 1 female, December 21–24, 1979 (Janzen); 1 male, December 30–31, 1980 (Janzen and Hallwachs). Additional specimens, not paratypical, include 1 male, 1 female, La Pacifica, 4 km NW Canas, Guanacaste Prov., May 29, 1973 (F. Cordero); 1 female, Managua, Nicaragua, May 1953 (Swain); 1 female, 8.6 mi W Managua, June 18, 1972 (R. R. and M. E. Murray).

Diagnosis. The absence of basal asperites and reduced numbers of orange patches of the elytra separate this subspecies from the typical one occurring from Panama southward. *L. t. costaricae* has a tendency to be grayish pubescent between the rounded patches. Variation within the type series is expressed in the amount and color of the ground pubescence. The irregular, median, white maculae are often reduced.

According to D. H. Janzen (pers. comm.) adults of *L. t. costaricae* girdle large stems of *Enterolobium cyclocarpum* (Jacq.) Griseb. and less commonly, *Pithecellobium saman* at Santa Rosa National Park in Costa Rica.

Received February 6, 1985; accepted June 17, 1985.

J. New York Entomol. Soc. 94(1):20–31, 1986

NEW LAMIINAE FROM MEXICO (COLEOPTERA: CERAMBYCIDAE)

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Abstract.—*Plagiohammus decorus, Cacostola janzeni, C. nelsoni, Lochmaeocles nigritarsus, L. crenatus, Eutrichillus brevipilus, Pseudostylopsis squamosus,* and *Dectes nigripilus* are described as new from Mexico. Dorsal view figures are provided for *P. decorus, L. nigritarsus,* and *L. cretatus.*

During the course of studies on North American Lamiinae, it became necessary to examine related groups in Mexico in order to determine distributional limits and relationships. A number of new taxa were discovered and eight of these are described below.

We gratefully acknowledge the following institutions and individuals for the loan of material: American Museum of Natural History; Essig Museum of Entomology, University of California, Berkeley; Field Museum of Natural History; Los Angeles County Natural History Museum; Ohio State University; Texas A&I University; Texas A&M University; University of California, Davis; University of Kansas; Utah State University and E. Giesbert, F. Hovore, and J. Wappes. Carolyn Tibbetts prepared the illustrations.

Plagiohammus decorus, new species

Fig. 1

Description. Male: Form large, slightly tapering; integument reddish brown and piceous; pubescence rosy gray, white and orange brown. Head with front coarsely, confluently punctate, densely clothed with appressed rosy gray pubescence, eyes narrowly outlined with rosy orange pubescence; vertex with several punctures along rear eye margins; genae much shorter than lower eye lobes, with a dull glabrous spot below eye; eyes large, lower lobes rounded, upper lobes separated by little more than width of lobes; antennal tubercles prominent; antennae about twice as long as body, scape almost cylindrical, usually dark, segments from third paler reddish brown, darker at apices, segments densely clothed with very fine, appressed rosy gray pubescence, segments to eighth with a fine fringe of suberect hairs beneath, third segment subequal to fourth, fifth shorter than fourth. Pronotum broader than long, sides with large, acute spines; disk with three rugose calluses, one median and one on each side before middle; post apical impression deep, sinuate; base broadly impressed, impression transversely rugose; pubescence dense, appressed, rosy gray, brownish gray along base, two white fasciae present along bases of lateral tubercles but not extending to basal margin; a few seta-bearing punctures present behind lateral tubercles and at sides of middle callus; prosternum impressed, densely rosy gray pubescent, intercoxal

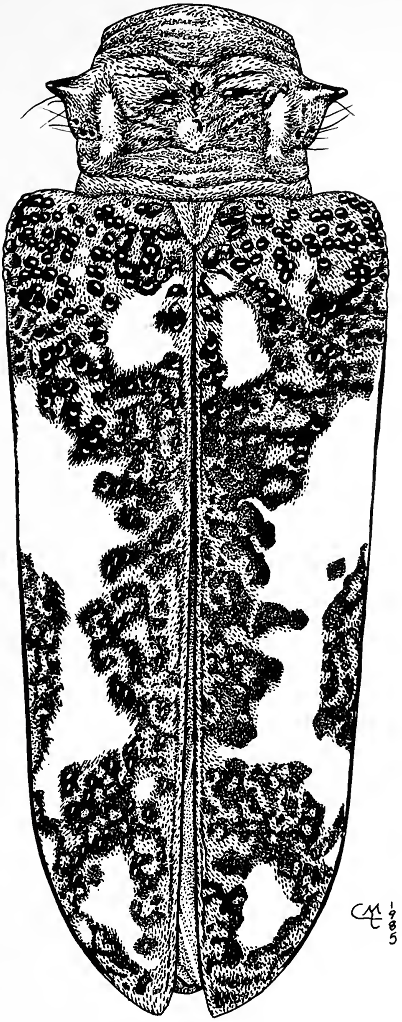

Fig. 1. *Plagiohammus decorus* Chemsak and Linsley, ♂.

process arcuate; mesosternum with intercoxal process abruptly declivous, produced above level of coxae; metasternum densely brownish gray pubescent, sides with small, thick pale spots. Elytra a little more than twice as long as broad; base rather densely covered with glabrous, granular punctures followed by deep coarse punctures near suture, becoming obsolete behind middle; base densely clothed with fine brown orange pubescence around granules, remainder of surface around white fasciae reticulate-pubescent, fasciae consisting of very dense white pubescence, two irregularly shaped spots near suture behind base, each side with a large, irregular edged lunate fascia extending from lateral margin behind humerus onto disk and to lateral margin at about apical one-third, two small fasciae present at middle before apex; apices narrow, not produced. Legs stout; femora sublinear, densely rosy gray and brownish gray pubescent; hind tibiae arcuate. Abdomen densely micropunctate; pubescence dense, rosy gray with longer white hairs intermixed; last sternite emarginate at apex. Length, 26–30 mm.

Female: Form more robust. Antennae a little longer than body. Abdomen with last sternite shallowly emarginate at apex, shallowly impressed longitudinally. Length, 29–30 mm.

Type material. Holotype male, allotype (California Academy of Sciences) and six paratypes (5 males, 1 female) (Essig Museum) from San Jeronimo, Chiapas, Mexico, 600 M, August 4–16, 1975; August 13, 1970; August 22, 1977.

Diagnosis. The lunate fasciae of the elytra have irregular margins and occasionally are divided medially. One male specimen in the series has the reticulate pubescence of the elytra paler and more gray than rosy as pubescence elsewhere.

P. laceratus (Bates) has a similar pattern of white fasciae but differs by having smaller basal granules on the elytra, more acute lateral tubercles of the pronotum, apically spined elytra, and also lacks the deep sinuate impression of the pronotum. In *P. lunaris* (Bates), the white fasciae are less irregularly margined, the elytral apices are spined and the glabrous spots of the elytra much smaller.

Cacostola janzeni, new species

Description. Male: Form moderate sized, slender; integument dark reddish brown; pubescence fine, short, appressed, grayish and brown. Head with front quadrate, finely, separately punctate, densely clothed with variegated grayish and brownish pubescence; genae short, less than ½ as long as lower eye lobes; antennal tubercles prominent, forming a broad V-shape from above, apices obtusely produced internally; antennae slender, a little longer than body, scape stout, third segment curved, segments from fourth darker over apical ½, gray pubescent on pale areas, segments with several suberect setae beneath, fourth segment slightly longer than third, fifth subequal to fourth, segments six to ten gradually diminishing in length, eleventh slightly longer than tenth. Pronotum broader than long, sides broadly rounded; apex shallowly impressed, base more deeply, broadly impressed; disk convex, middle with a vague longitudinal carina; punctures fine, dense, sparser at sides; pubescence fine, dense, appressed, mottled grayish and brown, sides near base with several long, erect setae; prosternum densely pubescent; meso- and metasternum densely pubescent, metasternum with scattered punctures. Elytra more than 2½ times as long as broad, sides slightly impressed near middle; each side with a glabrous carina extending from humeri to about middle; base shallowly bigibbose; punctures coarse, subconfluent, becoming a little finer toward apex; pubescence fine, short, appressed, mottled brownish and gray; apices rounded. Legs short; femora strongly clavate, micropunctate; pubescence fine, rather sparse. Abdomen subopaque, shallowly microsculptured; pubescence dense, mottled brownish and gray; last sternite shallowly emarginate at apex. Length, 8–10 mm.

Female: Form similar. Antennae about as long as body, last segment short. Abdomen with last sternite broadly, shallowly emarginate at apex, medially impressed. Length, 10 mm.

Type material. Holotype male (California Academy of Sciences) and three paratypes (1 male, 2 females) from Cotaxtla Experiment Station, Cotaxtla, Veracruz, Mexico, July 12, 1962 (D. H. Janzen). An additional male from 10 mi N Matias Romero, Oaxaca, July 3, 1975 (C. A., W. E., and B. W. Triplehorn) is also assignable to this species.

Diagnosis. The humeral carinae, shorter antennae, and mottled brownish and gray pubescence will separate *janzeni* from *salicicola* (Linsley). *C. rugicollis* Bates differs by its larger size, rugose pronotum and white vittae of the elytra. *C. mexicana* (Breuning) can be distinguished by the whitish vittae of the elytra and lack of humeral carinae.

We are pleased to dedicate this species to D. H. Janzen in recognition of his efforts in collecting Cerambycidae.

Cacostola nelsoni, new species

Description. Male: Form moderate sized, cylindrical; integument dark reddish brown, elytra paler; pubescence dense, fine, appressed, grayish with pale brown intermixed. Head with front quadrate, coarsely, rather densely punctate, densely clothed with grayish appressed pubescence; eyes small, lower lobes about as long as genae; antennal tubercles prominent, bases broadly divergent, apices acutely produced; antennae about 1½ times as long as body, scape conical, third segment slightly curved, segments from fourth pale over apical one-half, grayish pubescent, long, suberect setae numerous on third segment, becoming less numerous toward apex, fourth segment longer than third, fifth subequal to third, eleventh almost 1½ times longer than tenth. Pronotum broader than long, sides broadly rounded; apex shallowly impressed, base more deeply, broadly impressed; disk convex, coarsely, densely punctate; pubescence dense, mottled pale brownish and gray, middle with a vague, narrow, longitudinal grayish vitta, sides near base with several long, erect hairs; prosternum densely pubescent; meso- and metasternum densely clothed with fine, appressed pubescence. Elytra about 2½ times as long as broad, sides subparallel; disk convex, lacking basal gibbosities; punctures at base coarse, contiguous, becoming finer near apex; pubescence fine, short, appressed, grayish, vaguely brownish along suture; apices rounded. Legs short, densely grayish pubescent; femora strongly clavate. Abdomen densely pubescent; last sternite subtruncate at apex. Length, 11 mm.

Female: Form similar. Antennae a little longer than body. Abdomen with last sternite triangularly impressed, apex with dark setae. Length, 11–12 mm.

Type material. Holotype male (California Academy of Sciences) from 5 mi N Mazatlan, Sinaloa, Mexico, July 25, 1973 (Chemsak, Linsleys, and Michelbachers). Two female paratypes (Essig Museum, G. H. Nelson), same locality, August 10, 1965, July 18, 1972 (G. H. Nelson).

Diagnosis. This species is distinctive by the subparallel, paler elytra, rather uniform, fine grayish pubescence and coarsely, densely punctate pronotum.

C. nelsoni is dedicated to G. H. Nelson for his cooperation through the years.

Lochmaeocles nigritarsus, new species

Fig. 2

Description. Male: Form moderate sized, robust; integument piceous to reddish piceous; pubescence dense, appressed, grayish, brownish and brownish orange. Head with front quadrate, punctures sparse, scattered, pubescence orange and gray variegated, margins narrowly orange; median line glabrous, extending onto neck; vertex impunctate except for several punctures along eye margins, pubescence orange and gray variegated; antennal tubercles very prominent, curving downward and inward, bases forming a wide U; genae about as long as lower eye lobes, area beneath eyes pubescent; antennae slender, about 1½ times longer than body, scape moderately clavate, third and fourth segments densely fringed beneath, fifth sparsely fringed, segments finely, densely pubescent, grayish at apices, brownish beyond, third segment much longer than scape, fourth a little longer than scape. Pronotum much broader than long, lateral tubercles moderate, blunt, located behind middle; disk smooth, middle with a low glabrous callus before base, usually with a glabrous callus on each side slightly before median one; apex and base rather deeply impressed, apical impression broadened at middle; glabrous, setigerous punctures present behind middle at sides and on posterior sides of lateral tubercles; pubescence dense, mottled orange and gray; prosternum narrow, intercoxal process prominently produced at middle; meso- and metasternum densely gray pubescent at middle, sides mottled orange pubescent. Elytra less than twice as long as broad; base shallowly, broadly bigibbose; punctures behind base slightly asperate, not dense, rather fine and sparse behind, larger and scattered at sides at middle, becoming obsolete toward apex; humeri with a large glabrous callus; pubescence dense, appressed, immediate base gray followed by a broad brownish area which contains numerous, white outlined, orange spots, median white chevrons broad, extending from sides almost to suture, pubescence interrupted by a number of black punctures, posterior margins of chevrons narrowly bordered by brownish zig-zag fasciae, apical one-third brownish with numerous white-encircled orange spots; apices rounded. Legs stout; front coxae with a small dorsal tubercle; front femora gradually clavate, transversely rugulose basally beneath; femora mottled orange and gray pubescent, brownish annulate near apices; tibiae narrowly pale pubescent basally, remainder dark; tarsi black, thinly dark pubescent. Abdomen densely gray pubescent, sides and apices of sternites vaguely orange; sternites with small glabrous spots at sides; last sternite shallowly emarginate at apex. Length, 22–25 mm.

Female: Form similar. Antennal tubercles not projecting. Antennae a little longer than body. Abdomen with last sternite emarginate at apex, lightly fringed and narrowly impressed longitudinally. Length, 20–24 mm.

Type material. Holotype male, allotype (California Academy of Sciences) from X-Can, Quintana Roo, Mexico, June 1, 1968 (E. Welling). Paratypes (Essig Museum, E. Giesbert and J. Wappes) as follow: 3 males, 6 females, X-Can, May 13, 1969; June 1, 1969; May 21, 1969; June 1969; 1 female, Piste, Yucatan, June 26, 1969; 1 female, Piste, Mpio Tinum, Yucatan, June 14, 1977; 2 males, 5 females, 20 km N Carrillo Puerto, Quintana Roo, June 12–14, 1983 (E. Giesbert and J. Wappes); 2 males, 2 females, 18–24 km N San Felipe Carr. Pto., Quintana Roo, May 27–June 1, 1984 (Wappes); 1 female, 1 km W Cancun, Yucatan, June 9, 1983 (Wappes).

Diagnosis. The type series varies very little in coloration and pubescent pattern. Occasionally the head and pronotum are mottled with brownish rather than orange. The basal asperate punctures vary in number as do the glabrous punctures of the white chevrons of the elytra.

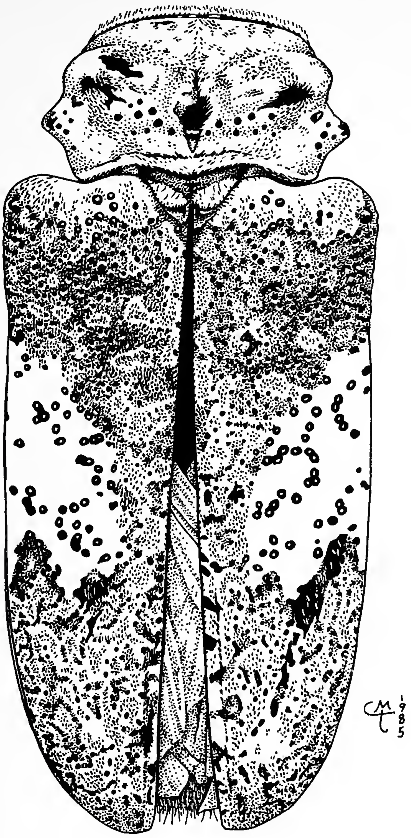

Fig. 2. *Lochmaeocles nigritarsus* Chemsak and Linsley, ♂.

This species is distinctive by the strongly produced middle of the prosternal process, the color pattern of the elytra and the black tarsi. The other species with a similar prosternal character differ considerably in the elytral color pattern.

Lochmaeocles cretatus, new species

Fig. 3

Description. Male: Form moderate sized to large, robust; integument piceous to dark reddish brown; pubescence dense, appressed, white, orange and brownish. Head with front quadrate, punctures sparse, scattered, pubescence mottled orange and gray, margins and each side of median line densely orange pubescent, eyes rather vaguely margined behind with pale orange; median line glabrous, extending onto neck; vertex impunctate, with a short carina along edges of upper eye lobes, pubescence grayish with two vague brownish spots at middle; eyes moderate, lower lobes about as long

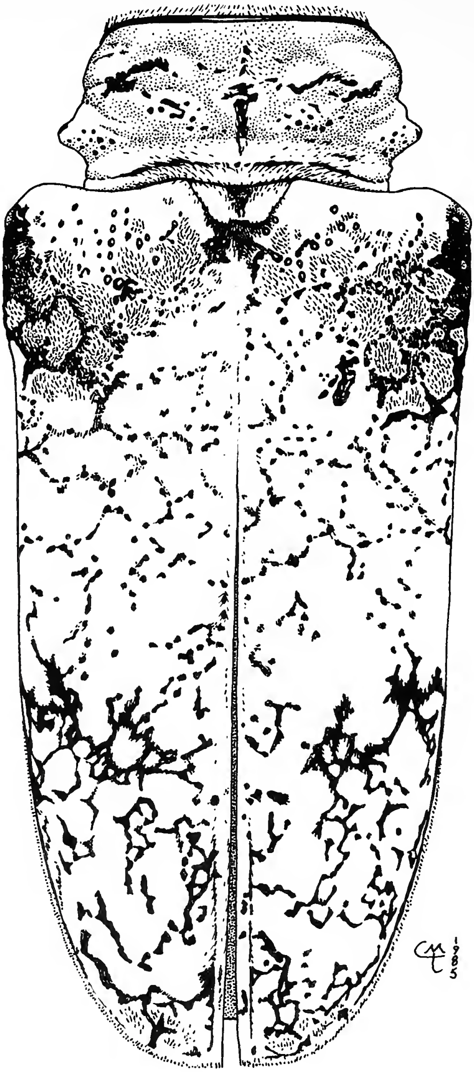

Fig. 3. *Lochmaeocles cretatus* Chemsak and Linsley, ♂.

as genae; antennal tubercles prominently produced, curved, extending inward and downward, bases forming a broad U; antennae slender, about 1½ to 2 times longer than body, scape feebly clavate, third segment densely fringed beneath, fourth sparsely fringed, fifth with several suberect hairs, segments very finely, densely grayish pubescent, scape basally rugose, third segment much longer than scape, fourth shorter than third, fifth shorter than fourth. Pronotum much broader than long, lateral tubercles blunt, located before base; disk with a median callus and two broad, transverse calluses on each side just before middle; apex deeply impressed, impression broadening at middle; base shallowly impressed; pubescence dense, grayish, often vaguely suffused with brownish; punctation absent except for a few, glabrous, setigerous punctures on posterior half of lateral tubercles and posterior margins of lateral dorsal calluses; prosternum densely grayish pubescent, intercoxal process arcuate, not medially produced; meso- and metasternum densely gray pubescent, sides tinged with orange. Elytra about twice as long as broad, slightly tapering posteriorly; base shallowly bigibbose; punctures behind base finely asperate, rather sparse, dense behind humeri, punctures behind sparse, fine, irregularly linearly arranged; humeri with a large glabrous callus; pubescence dense, appressed, somewhat reticulately interrupted by glabrous punctures, immediate base whitish followed by a broad band of mostly orange patches, remainder of elytra mostly reticulate whitish, usually with irregular, narrow orange and/or brown chevrons behind middle which do not extend to suture, apical portion often slightly suffused with orange; apices rounded. Legs stout; front coxae with a dorsal tubercle; front femora sublinear, very gradually expanding toward apex, basally rugose internally; femora gray pubescent dorsally, front pair often suffused with orange and with a V-shaped brown vitta near apex, middle and hind pair orange suffused beneath with a brown V-shaped apical vitta; tibiae orange and gray pubescent; tarsi dark. Abdomen densely gray pubescent, sternites with small glabrous spots at sides; last sternite truncate at apex, vaguely emarginate at middle. Length, 21–30 mm.

Female: Form similar, elytra subparallel. Antennal tubercles not strongly projecting. Antennae a little longer than body. Legs with front not tuberculate, front femora normal. Abdomen with last sternite emarginate at apex, lightly fringed, medially impressed longitudinally. Length, 22–28 mm.

Type material. Holotype male, allotype (California Academy of Sciences) and nine paratypes (4 males, 5 females) from 20 km N Carrillo Puerto, Quintana Roo, Mexico, June 12–14, 1983 (E. Giesbert and J. Wappes); additional paratypes as follows: 1 male, 2 females, 1 km S Xcalacoop, Yucatan, June 11, 1983 (Giesbert and Wappes); 1 female, Chichen Itza, Yucatan, June 10–11, 1983 (Giesbert); 1 female, Kantunil, Yucatan, April 1977 (E. Welling); 1 female, Piste, Mpio Tinum, Yucatan, June 13, 1977 (Welling); 1 male, 2 females, 18–24 km N San Felipe Carr. Pto., Quintana Roo, May 27–June 1, 1984 (Wappes); 1 female, Nuevo X-Can, Quintana Roo, May 28, 1976 (Welling). An additional male from "S. Mex." is also at hand. Paratypes in collections of Essig Museum, E. Giesbert and J. Wappes.

Diagnosis. The dense, whitish pubescence of the elytra with the basal orange band make this species distinctive. The narrow post median vittae are often vague and the apical portions of the elytra are varyingly suffused with orange.

Eutrichillus brevipilus, new species

Description. Male: Form small, tapering apically; integument piceous, appendages and underside partially reddish brown; pubescence fine, dense, appressed, brownish, gray and black, erect setae of elytra about as long as width of antennal scape. Head with front short, transverse, densely micropunctate, pubescence dense, mottled gray and brown; vertex micropunctate, dark pubescent medially behind eyes; eyes moderate, lower lobes a little shorter than genae, upper lobes widely separated; antennae about 1½ times longer than body, scape dark beneath, remaining segments dark at apical ½ or more, segments to sixth with several suberect setae beneath, pubescence fine, thin, scape pale annulate at middle, segments three to six pale biannulate, remaining segments pale pubescent at apices, third segment longer than scape, fourth subequal to scape. Pronotum broader than long, sides acutely tuberculate behind middle, spines directed back; disk with three low calluses; punctures moderately coarse, scattered, denser on basal impression; pubescence dense, grayish, with a vague dark vitta on each of middle and a shorter median one, sides with a few long, erect setae behind lateral tubercles; prosternum finely, thinly pubescent; meso- and metasternum finely, densely punctate, densely clothed with grayish depressed pubescence. Elytra a little more than twice as long as broad; base feebly bigibbose; costae vague; punctures moderately coarse, dense, becoming finer toward apex; pubescence dense, grayish, with black tufts present on gibbosities and two behind middle, one pair near suture and another on disk, small dark spots and tufts scattered along costae and lateral margins giving a mottled appearance; suberect setae short, numerous; apices narrowly subtruncate. Legs with femora strongly clavate, finely grayish pubescent, dark biannulate near apices; tibiae pale annulate at base and middle; tarsi slender, pale pubescent at apices of first two segments. Abdomen densely, minutely punctate, moderately densely gray pubescent; last sternite emarginate at apex. Length, 5.5–8 mm.

Female: Form similar. Antennae slightly shorter. Abdomen with last sternite about as long as two preceding segments together, apex narrow, emarginate. Length, 7–9 mm.

Type material. Holotype male, allotype (California Academy of Sciences) from 3 mi W El Salto, Durango, Mexico, 9,000 ft, July 18, 1964 (J. A. Chemsak). Paratypes as follow: 2 males, 3 mi W El Salto, July 22–23, 1964, ex. *Quercus* (Chemsak); 1 female, 5 mi W El Salto, May 4, 1961, ex. *Quercus* (Howden and Martin); 1 male, 9 mi E La Ciudad, Durango, 9,000 ft, July 20, 1964, ex. *Quercus* (Chemsak). Paratypes in Essig Museum and Canadian National Collection.

Diagnosis. This species is sympatric with *E. pini* (Schaeffer) and probably *E. neomexicanus* (Champlain and Knull) but appears to utilize *Quercus* instead of *Pinus* as a host. The shorter elytral setae and color pattern of the elytra will separate *brevipilus* from either of those species.

Pseudastylopsis squamosus, new species

Description. Male: Form moderate sized, elytra tapering at apical one-third; integument piceous and dark reddish brown; pubescence dense, short, dorsally scale-like, gray, brownish and black. Head with front rectangular, longer than broad, finely densely punctate, densely clothed with variegated brownish and grayish pubescence; vertex variegately pubescent, usually with two dark spots at middle at base; genae subequal in length to lower eye lobes; upper eye lobes separated by about diameter of antennal scape; antennae extending about four segments beyond body, scape impressed near apex, segments finely pubescent, scape irregularly pale annulate, segments 3–5 dark at apices, segments 6–10 dark, pale annulate medially, eleventh segment dark, third segment longer than first, fourth shorter than third, slightly longer than first, eleventh shorter than tenth. Pronotum broader than long, sides obtusely tuberculate behind middle; apex narrower than base, narrowly impressed; base broadly impressed; disk with three calluses, one median and two larger behind apical impression; punctures coarse, placed around calluses and along impressions; pubescence short, scale-like, gray and brown variegated, calluses dark, base with three dark spots; prosternum thinly pubescent, intercoxal process almost one-half as broad as coxal cavities; meso- and metasternum densely pubescent, pubescence interrupted by glabrous spots, mesosternal process about as broad as coxal cavities, metasternum with a densely pubescent patch at middle. Elytra about twice as long as broad, tapering at apical one-third; base with two, crested gibbosities; costae distinct, joining before apex, inner pair beginning behind impressions, two outside pairs beginning near humeri and diverging; tufted tubercles present along costae, a pair near suture behind basal gibbosities, inner pair at apical one-third larger; pubescence short, scale-like, pale brownish at bases of black tubercles, dark spots present along suture behind impressions, apical one-third with a vague, whitish, oblique vitta, dorsal impressions often lightly suffused with white; punctures coarse, separated, becoming finer near apex; apices narrowly rounded. Legs rather robust; femora pale pubescent with small dark spots interspersed, apices dark; tibiae pale annulate at bases and middle; tarsi dark. Abdomen densely grayish pubescent, pubescence interrupted by small glabrous spots; last sternite longer than fourth, apex narrow, emarginate. Length, 8–11 mm.

Female: Form similar. Metasternum lacking a densely pubescent patch. Abdomen with last segment elongate, extending well beyond elytra, apex with numerous long setae. Length (exclusive of ovipositor), 9–10 mm.

Type material. Holotype male, allotype (California Academy of Sciences) from El Palmito, Sinaloa, Mexico, August 7–8, 1983 (F. Hovore), August 2, 1983 (E. Giesbert). Paratypes as follow: 1 female, El Palmito, August 3, 1983 (Giesbert; 1 female, 2–7 km W El Palmito, August 3, 1983 (Giesbert); 1 male, 30 km W El Palmito, October 18–21, 1978 (Giesbert); 3 males, Loberas, Hwy 40, Sinaloa, August 7, 1983 (Hovore); 1 female, 24 mi W La Ciudad, Durango, 7,500 ft, July 19, 1964, ex *Pinus* (J. A. Chemsak); 1 male, 14 mi SW El Salto, Canyon, Durango, August 3, 1964, ex *Pinus* (Chemsak). Paratypes in collections of Essig Museum, F. Hovore and E. Giesbert.

Diagnosis. Although superficially similar to *P. pini* (Schaeffer), this species can be readily separated by the short, scale-like pubescence of the pronotum and elytra and the vague whitish vitta at the apical one-third of the elytra. The presence of the pubescent patch on the metasternum of males and the elongate last abdominal segment of females will further differentiate *squamosus* from *pini.*

The type series varies in coloration with more black pubescence often present on the pronotum and elytra.

Dectes nigripilus, new species

Dectes texanus aridus: Dillon, 1956. Ann. Entomol. Soc. Amer. 49:355 (part).

Description. Male: Form small; integument black; elytra densely clothed with very fine, black, appressed pubescence. Head with front densely micropunctate, densely clothed with grayish appressed pubescence; genae shorter than lower eye lobes, antennae extending about three segments beyond elytra, segments finely dark pubescent dorsally, finely grayish pubescent ventrally, scape subequal to third segment, second segment a little longer than broad, fourth shorter than third. Pronotum a little broader than long, lateral spines prominent, directed back; disk convex, densely micropunctate with larger punctures moderately interspersed, middle near base with a narrow longitudinal callus; pubescence dense, fine, dark, with several long setae on bases of lateral tubercles and behind on margins; prosternum moderately densely grayish pubescent; metasternum densely clothed with long, suberect, grayish pubescence at middle. Elytra more than 2½ times longer than broad; punctures dense, contiguous, a little larger than those of pronotum; pubescence dark, very short, appressed, black, suberect setae numerous; apices broadly rounded. Legs finely, densely grayish and dark pubescent; tarsi with scattered grayish pubescence. Abdomen densely, finely punctate; pubescence, fine, short, grayish; last sternite emarginate at apex, middle with dark setae. Length, 5–10 mm.

Female: Form similar. Abdomen with last sternite longer than fourth, narrowly truncate at apex. Length 6–10 mm.

Type material. Holotype male and allotype (University of California, Davis) from Petlalcingo, Puebla, Mexico, August 3, 1963 (F. D. Parker and L. A. Stange). Paratypes all from Mexico as follow: 17 males, 12 females, 3 mi N Petlalcingo, August 3, 1963 (Parker and Stange); 3 males, 5 females, 11 mi SE Acatlan, Puebla, July 10, 1952 (E. E. Gilbert and C. D. MacNeil); 1 female, Puebla, 7,200 ft, August 22, 1957 (H. A. Scullen); 1 male, 2 females, San Juan Teotihuacan, Puebla, July 28, 1947 (B. Malkin); 1 male, Monte Alban, Oaxaca, September 14, 1947 (Malkin); 1 female, 3 mi SE Yanhuitlan, Oaxaca, September 17, 1974 (G. Bohart and W. Hanson); 1 male, 1 female, Madera, Chihuahua, 7,200 ft, July 6, 1947 (Speith); 1 male, 12 mi W Hidalgo del Parral, Chihuahua, 6,200 ft, on *Cucurbita foetidissima,* July 14, 1964 (J. A. Chemsak); 1 female, 1 mi SW Yerbanis, Durango, August 12, 1965 (H. Burke and J. Meyer); 1 female, Comonfort, Guanajuato, August 12, 1953 (C. and P. Vaurie); 1 male, 2 females, 2 mi W La Barca, Jalisco, July 24, 1966 (P. M. and P. K. Wagner); 1 female, 28 mi SW Guadalajara, Jalisco, September 6, 1972 (B. Villegas and E. A. Kane); 1 female, 4 mi W Mazamitla, Jalisco, 6,800 ft, October 16, 1950 (R. F. Smith); 1 male, 1 female, 39 km W Toluca, Mexico, 8,300 ft, July 17, 1965 (R. E. Snelling); 1 male, 1 female, Toluca, August 1903; 2 males, Morelia, Michoacan, September 4, 1938 (L. J. Lipovski); 1 female, 14 mi SW Pachuca, Hidalgo, 7,500 ft, July 9, 1961 (U. Kans. Mex. Exped.); 1 male, Mexico City, September 2, 1939 (Painter); 1 male, 1 female, Chapingo, Mexico (F. Pacheco); 1 male, Texcoco, Mexico, August 12, 1954 (U. Kans. Mex. Exped.); 1 female, Atlacomulco, Mexico, 8,800 ft, August 18, 1954 (U. Kans. Mex. Exped.); 1 male, 2 females, 10 mi Atlacomulco, 8,100 ft, August 18, 1954 (U. Kans. Mex. Exped.); 1 female, 22 mi N Atlacomulco, 8,100 ft, August 18, 1954 (C. D. Michener); 1 male, 23.6 mi NW Zacatlan, Hidalgo, 6,650 ft, August 22, 1962 (U. Kans. Mex. Exped.); 1 female, Teotihuacan, Mexico, July 21, 1956 (R. and K. Dreisbach); 1 female, Guadalupe, Hidalgo, July 2, 1932; 1 female, Victor Rosales, Zacatecas, September 6, 1951 (J. J. McKelvey). Paratypes in collections of Essig Museum, American Museum of Natural History, Field Museum of Natural History, Los Angeles County Natural History Museum, Ohio State University, Texas A&I University, Texas A&M University, University of California, Davis, University of Kansas and Utah State University.

Diagnosis. This species may be immediately separated from *D. texanus* LeConte by the totally black coloration, presence of very fine, short, black pubescence on the elytra, and by the suberect pubescence of the metasternum. All specimens of *texanus* possess thicker, grayish, appressed pubescence on the entire body.

D. nigripilus varies considerably in size but the coloration is rather constant. Often the legs and underside are more dark pubescent. This species is sympatric with *texanus* over most of its range and appears to occur at higher elevations.

Received February 27, 1985; accepted June 17, 1985.

J. New York Entomol. Soc. 94(1):32–38, 1986

A REVIEW OF *ACETROPIS AMERICANA* KNIGHT IN NORTH AMERICA (HEMIPTERA: MIRIDAE: STENODEMINI)

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Abstract.—*Acetropis americana* Knight, from the Willamette Valley of Oregon, is compared with *A. longirostris* Puton of eastern Europe and they are recognized as sister species. The male, female and nymphal habitus and male and female genitalia of *americana* are presented.

The genus *Acetropis* Fieber currently contains seven species placed in two subgenera (Wagner, 1967; Stys, 1973). The subgenus *Acetropis* consists of *americana* Knight, 1927; *carinata* (Herrich-Schaeffer, 1841); *gimmerthali gimmerthali* (Flor, 1860); *gimmerthali parva* Wagner, 1968; *josifovi* Wagner, 1967; *longirostris* Puton, 1875; *sinuata* Wagner, 1951. The subgenus *Paracetropis* Wagner, 1962 is monotypic, containing *atropis* Reuter, 1895. Six species are found in the western Palearctic Region while the seventh, *A. americana* Knight, is known only from western Oregon in North America (Knight, 1927; Slater and Baranowski, 1978). The Old World species are found throughout Europe (Southwood and Leston, 1959; Wagner, 1958, 1967, 1968; Wagner and Weber, 1964), including southern Russia (Kerzhner and Jaczewski, 1964), North Africa (Wagner, 1962), and Turkey (Hoberlandt, 1955). This genus occurs on grasses, but few specific host plants have been identified. Southwood and Leston (1959) report *A. gimmerthali* (Flor) on *Arrhenatherum elatinus* (L.) in England, Koppányi (1965) reports *A. longirostris* Puton on *Alopercurus pratensis* (L.) in Hungary, and the senior author collected *A. carinata* (H.-S.) on *Festuca ovina* L. in the Netherlands.

Knight (1927) described *A. americana* from Corvallis, Oregon, based on specimens collected by A. C. Burrill and C. J. Drake. Drake reported that he thought the specimens were taken on "a wild oat grass" (we surmise that this grass species is *Deschampsia cespitosa* [L.] Beauv. var. *arctica* Vasey, a rare native grass of wet habitats) (females only, collected in late June). No additional specimens were collected until 1946. Other specimens were collected in 1959 on the southwest edge of Corvallis in a low, wet grassland. This site was subsequently filled and the habitat destroyed. Several specimens were also collected along the Yamhill River, near McMinnville in late May 1958. Another site was located, at Finley Wildlife Refuge, 10 miles south of Corvallis. This locality is another low, wet grassland. Nymphs and a few adults have been collected from Finley but have not been abundant enough to allow positive host plant association. This site, and the previously existing locality in Corvallis, appeared relatively undisturbed—a rarity in the Willamette Valley where most grasslands now contain introduced species.

Although Knight (1927) described the species as new, we had considered it to be an introduced species, most likely from western Europe. It has long been known that several other stenodemines species in eastern North America are Palearctic introductions (Osborn, 1918; Knight, 1921; Slater, 1956). A number of introduced grass-feeding mirid species in the Systematic Entomology Laboratory of Oregon State University have been collected in the Willamette Valley including *Leptopterna dolobrata* (L.), *Megaloceraea recticornis* (Geoffroy), *Stenotus binotatus* (F.) and *Capsus ater* (L.) (Lattin and Oman, 1983; Lattin and Schwartz, unpubl. data). Knight compared *A. americana* with *A. carinata* (H.-S.) from western Europe. He did not consider the possibility of an accidental introduction but speculated that *americana* was the result of a natural invasion into North America from the Palearctic Region via Beringia at a time sufficiently long ago to allow the formation of a distinct species.

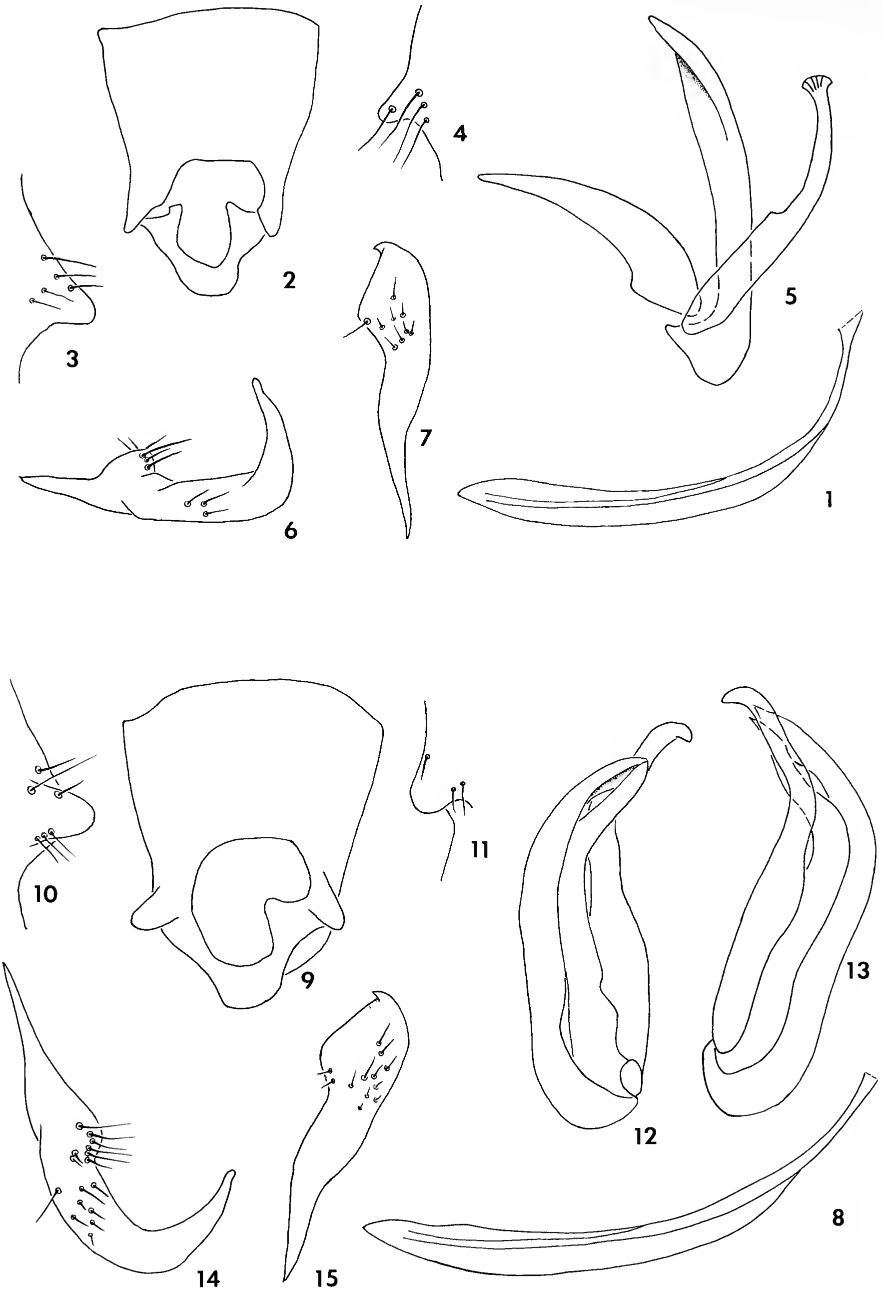
Lattin compared the Oregon material with the European species while working with Professor Dr. Rene H. Cobben at the Landbouwhogeschool in Wageningen, Netherlands in 1973–1974. The presence of three spiculae in the vesica clearly separated *americana* from *carinata* and *gimmerthali.* Professor Dr. Pavel Stys, Charles University, Prague, Czechoslovakia, kindly sent specimens of the central European species *A. longirostris* Puton. While *longirostris* is the only other species in *Acetropis* beside *americana* with three spiculae in the vesica, the two taxa did not seem conspecific and the apparent disjunction seemed real.

Schwartz has examined all species of *Acetropis* in the course of his work on the Stenodemini, including *A. americana* and *longirostris,* and reached the same conclusion; that *americana* represents the sister species of *longirostris.*

Several characters separate the two species. In females the anterior valvula of *americana* (Fig. 1) is shorter, with the distal portion stout and rounded compared to *longirostris* (Fig. 8), which is longer and more elongate and acuminate. Males of *americana* are distinguished from males of *longirostris* by the smaller genital capsule (Fig. 2) with the posteriorly directed genital tubercles (posterodorsal processes of Stys, 1973) (Figs. 3, 4), and the smaller spiculae with the dorsal one sublinear and broadly truncate apically (Fig. 5). The capsule of *longirostris* is longer (Fig. 9) with dorsolaterally directed tubercles (Figs. 10, 11), and the spiculae are somewhat larger with the dorsal one broadly curved with a recurved apex (Figs. 12, 13). The parameres of both species are quite similar (Figs. 6, 7 for *americana,* Figs. 14, 15 for *longirostris*). We have included a dorsal habitus of both sexes and the nymph (Figs. 16–18). On the basis of the sunken vertex *americana* is placed in the subgenus *Acetropis* of Wagner (1962).

No species of *Acetropis* are known from the eastern Palearctic Region. While there is a possibility that *Acetropis americana* does represent an introduction of a species not yet known from the Palearctic Region, this seems unlikely. Dr. I. M. Kerzhner, Zoological Institute, Leningrad, Soviet Union, has examined specimens of *americana* for us, and concurs that this species is not conspecific with *longirostris,* and that the genus *Acetropis* does not occur in central or eastern Asia.

The exclusive occurrence of *americana* in Finley Wildlife Refuge and Jackson-Frazier Wetlands indicates that this mirid is a bona fide native species. The relative rarity of *americana* only reflects the scarcity of undisturbed, wet native grasslands in the Willamette Valley of western Oregon. When positive host and/or habitat requirements have been determined, the question may be resolved. Further, *americana* might be taken in southwestern Washington if suitable sites could be located.



Figs. 1–15. 1–7. *Acetropis americana.* 8–15. *Acetropis longirostris.* 1, 8. Anterior valvulae of ♀, lateral view. 2, 9. Genital capsule of ♂, dorsal view. 3, 10. Left genital tubercle, lateral view. 4, 11. Right genital tubercle, lateral view. 5, 12, 13. Spicula of vesica, lateral view. 6, 14. Left paramere, lateral view. 7, 15. Right paramere, lateral view.

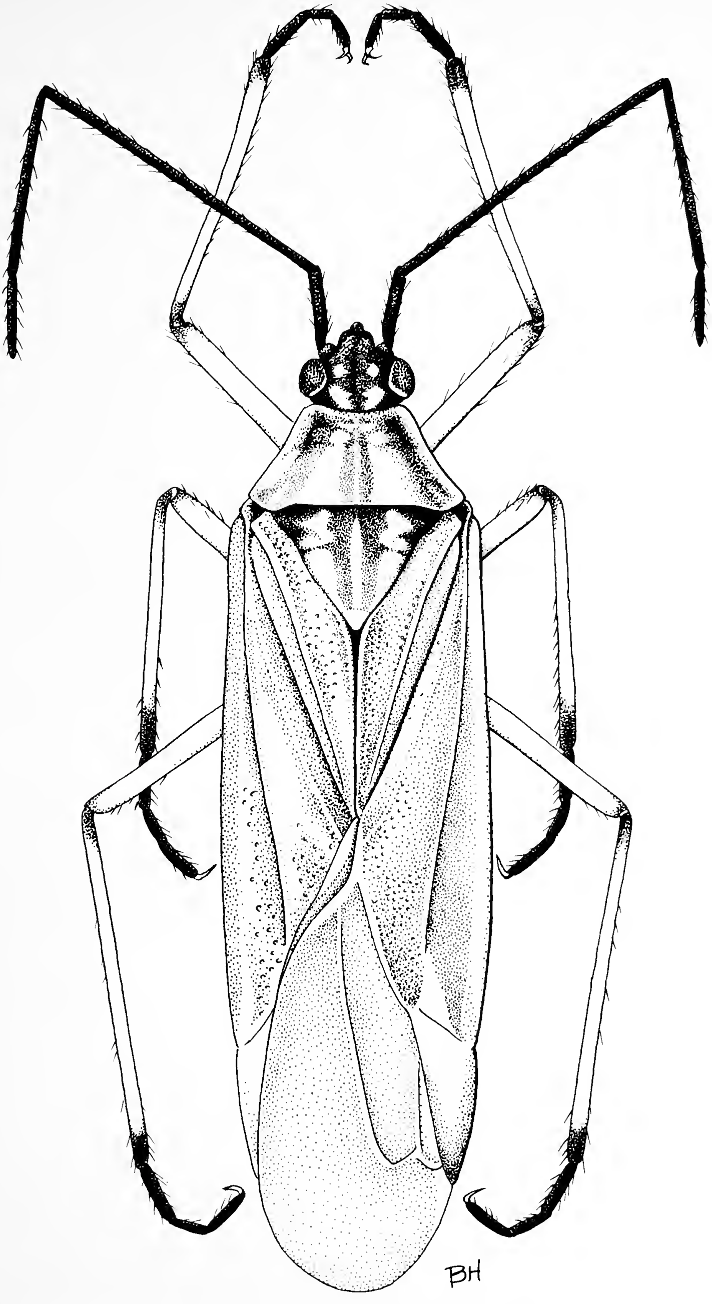
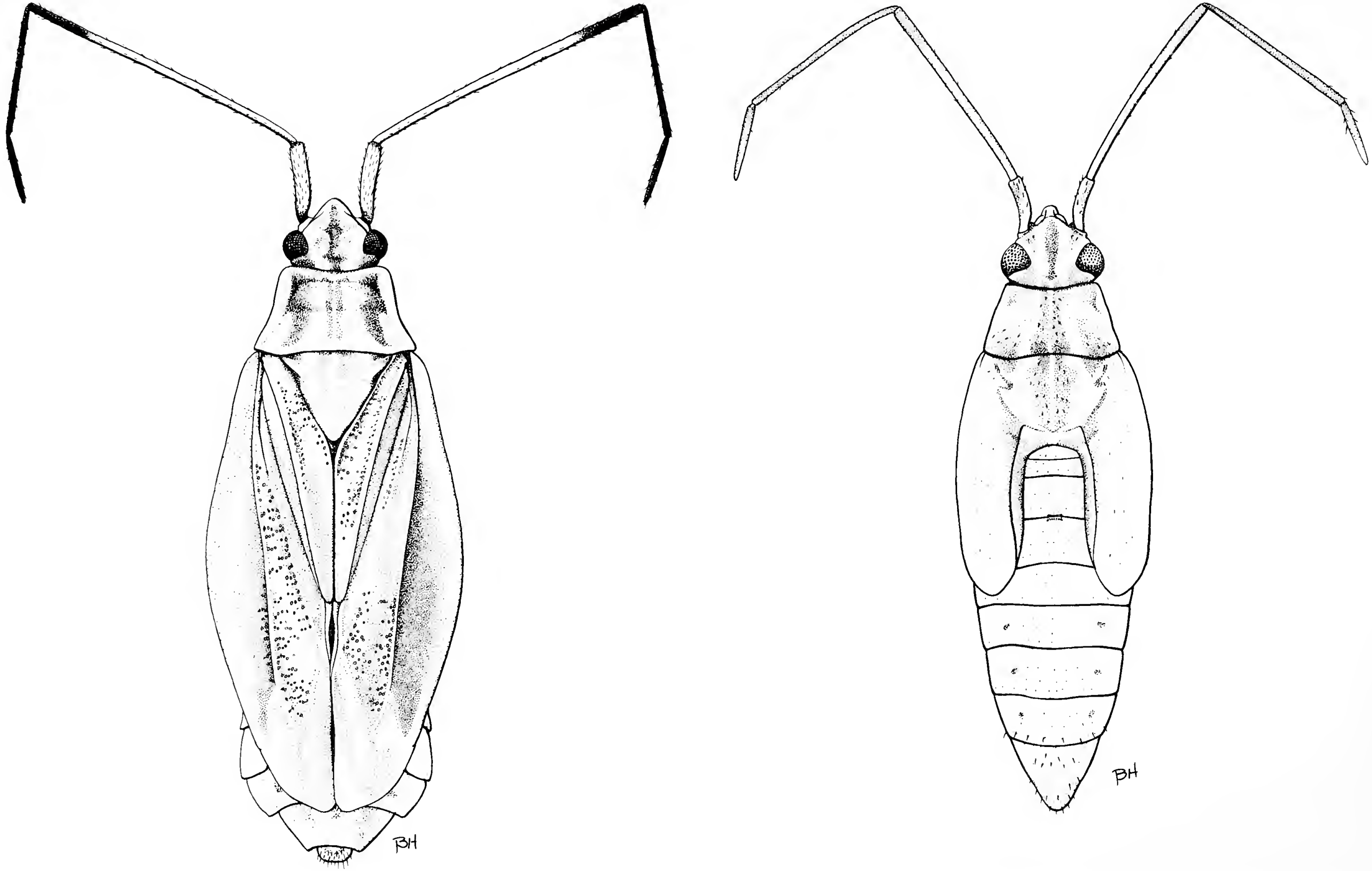


Fig. 16. Dorsal habitus of adult ♂ *Acetropis americana.*



Figs. 17, 18. Dorsal habitus of *Acetropis americana.* 17. Adult ♀. 18. Nymph.

Specimens examined. OREGON. *Benton Co.,* Corvallis: May 24, 1946, V. D. Roth, ♂ (OSU); study site, May 28, 1972, C. A. Musgrave, ex poplar, 2♂♂ (OSU); May 30, 1912, 1♂ (USNM); June 16, 1959, J. D. Lattin, 1♂, 1♀ (OSU); June 26, 1926, C. J. Drake, 1♀ allotype and 2♀♀ paratypes (USNM); July, A. C. Burrill, 1♂ holotype and 1♂ paratype (USNM). Finley Wildlife Refuge, May 21, 1977, J. D. Lattin, 4th and 5th instar nymphs (OSU); May 29, 1977, B. Searles, 4th and 5th instar nymphs (OSU); June 9, 1976, W. N. Mathis, 1♂ (OSU); June 21, 1977, B. Searles, ex grass, 1♂, 5♀♀ (OSU); June 27, 1977, G. Eulenson, ex grass, 2♀♀ (OSU). Jackson-Frazier Wetlands (NE Corvallis), June 7, 1985, J. D. Lattin, ex grasses, 1♂ (OSU). *Yamhill Co.,* Yamhill River, McMinnville, May 30, 1958, K. Fender, 2♀♀ (OSU).

ACKNOWLEDGMENTS

We wish to thank Ms. Bonnie B. Hall of the Systematic Entomology Laboratory, Oregon State University (OSU), for the habitus illustrations and Dr. Gary M. Stonedahl for reviewing the manuscript. Specimens for comparison were loaned from the United States National Museum, Washington, D.C. (USNM) by Dr. Richard C. Froeschner and Mr. Thomas J. Henry. Grateful acknowledgment is made to the Fulbright Commission and to the Netherlands Organization for Pure Scientific Research (ZWO) for partial support during 1973–1974 (JDL).

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Received June 6, 1985; accepted July 10, 1985.

J. New York Entomol. Soc. 94(1):39–50, 1986

NAUCORIDAE (HEMIPTERA) OF NEW GUINEA.
2. A REVIEW OF THE GENUS *IDIOCARUS* MONTANDON, WITH DESCRIPTIONS OF THREE NEW SPECIES

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Abstract.—The genus *Idiocarus* is reviewed based on recent collections in Papua New Guinea. Three new species, *I. isolatus, I. sepikanus,* and *I. papuus* are described, distribution notes are given for three previously described species, and a key to all species is provided, accompanied by figures of the male and female genital structures. *Idiocarus litus* La Rivers is reduced to a junior synonym of *I. elongatus* Montandon.

The genus *Idiocarus* was proposed by Montandon (1897) to contain *I. elongatus* from southeastern New Guinea, and the genus as a whole appears to be confined to the upland areas of that island. La Rivers (1971) added three additional species, *I. intermedius, I. litus,* and *I. minor,* and provided a key to the species. That key, however, is of limited usefulness, being based on superficial characters and accompanied by but a single habitus illustration. Our recent collections in Papua New Guinea have revealed three new species, *I. isolatus, I. sepikanus,* and *I. papuus,* which are described herein; we also provide a new key to the species in the genus and illustrations of the male and female genitalia.

Idiocarus is a member of the subfamily Cheirochelinae as defined by Usinger (1938, 1941), with the anteclypeus produced anteriorly over the labrum and the vertex produced posteriorly behind the eyes. The head modifications of *Idiocarus* species are much less developed than in other cheirocheline genera, particularly the anteclypeus which barely projects beyond the apex of the well-developed labrum. The maxillary plates lie in a vertical plane, with their pointed tips produced and nearly reaching the anterior anteclypeal apex, a condition not encountered elsewhere in the Cheirochelinae. In most populations the majority of individuals are brachypterous, with wing pads reaching only to the third abdominal segment. Among macropterous individuals, the wing membrane frequently disintegrates over time, leaving only the pointed hemelytra in a condition approximating brachyptery. The abdominal venter bears several unique structures, including depressed ovate areas of shining hairs laterally on the paratergites, raised hair clumps covering the spiracles, and paired slit-like openings in the hydrofuge pile near the inner margins of the paratergites. These modifications are similar to structures observed in the Neotropical genus *Cryphocricos* (Parsons and Hewson, 1974), and may serve in a similar role as hydrostatic pressure receptors. The morphological resemblances between the two

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genera are striking, originally leading Montandon (1897) to place both in his subfamily Cryptocricinae, but this resemblance would appear to be the result of convergent evolution in similar environments, since a character analysis indicates that *Cryphocricos* is allied to *Cataractocoris* and other Neotropical genera presently held in the Ambrysinae while *Idiocarus* is allied to *Sagocoris* and other primitive members of the Asian Cheirochelinae.

Externally, most species of *Idiocarus* are quite similar, differing primarily in habitus characteristics that are difficult to express in a key. Although external characters are employed in the key, workers should anticipate that these may prove unstable, and dissection of the male genitalia is recommended for definitive identification. At present scant material is available from the Indonesian province of Irian Jaya, comprising the western half of New Guinea, and it is anticipated that future collections in this region will yield additional undescribed species.

Idiocarus species are found under small to moderate sized stones in cool, swiftly flowing streams at elevations ranging from 200 to 1,700 meters (ca. 500 to 5,000 feet) above sea level. This genus was not encountered in the very cold mountain streams above this elevational range, where species of the allied genus *Tanycricos* were abundant, or at low elevations in the coastal ranges, where freshwater crabs and other crustaceans occupy typical *Idiocarus* habitats. Plastron respiration is unknown in any of the New Guinea Naucoridae, but may occur in *Idiocarus* species considering their habitat and morphological resemblance to the genus *Cryphocricos* in which plastron respiration is known (Parsons and Hewson, 1974). In particular, the prevalence of brachyptery and presence of apparent hydrostatic pressure receptors in both genera argues for such a convergence.

All material cited in this paper is held in the J. T. Polhemus collection (JTP) unless otherwise noted; all new species types are deposited in the Bishop Museum, Honolulu (BPBM). We are indebted to Dr. P. H. Arnaud, California Academy of Sciences, San Francisco (CAS), Dr. C. L. Hogue, Los Angeles County Museum (LACM); Dr. W. R. Dolling, British Museum (Natural History), London (BMNH), and Dr. P. H. van Doesburg, Rijksmuseum Van Natuurlijke Historie, Leiden (RNHL) for the loan of specimens. Proportions are given in units, with 40 units = 1 mm. CL numbers refer to codes used by the authors to reference ecological notes. This research was supported by a grant from the National Geographic Society, Washington, D.C.

KEY TO THE SPECIES OF *Idiocarus* MONTANDON

1. Prosternal carina prominent, ridge-like, shining and uninterrupted; female subgenital plate bearing hair tufts basally (Fig. 13); male left paramere with tip enlarged, rounded (Fig. 6); small species, overall length 8 mm or less .... *I. minor* La Rivers

– Prosternal carina not forming a prominent shining ridge over most of its length, interrupted at least once by shallow transverse sulci; female subgenital plate with or without hair tufts basally; male left paramere with tip not greatly enlarged, though often hooked (Figs. 2–5, 7); overall length usually exceeding 8 mm 2

2. Fore femur lacking raised black tubercles on anterior portion of dorsal face; female subgenital plate with hair tufts basally (Fig. 10); male left paramere gently curving, tip slender (Fig. 4); brachypterous forms usually reddish, frequently with tip of abdomen upturned .... *I. intermedius* La Rivers

– Fore femur bearing raised black tubercles on anterior portion of dorsal face; female subgenital plate lacking basal hair tufts; male left paramere with tip rounded or hooked, not slender and tapering (Figs. 2, 3, 5, 7); brachypterous forms generally brown or yellowish with dark mottling, not reddish, tip of abdomen usually not upturned 3

3. Posterior margin of female fifth abdominal sternite sinuate (Fig. 8); male left paramere with long straight arm, tip rounded (Fig. 2) .... *I. papuus,* new species

– Posterior margin of female fifth abdominal sternite smoothly curved or straight (Figs. 9, 11, 12); tip of male left paramere more or less hooked (Figs. 3, 5, 7) 4

4. Ventral face of fore femur bearing prominent raised black tubercles anteriorly; large, robust species, overall length clearly exceeding 10.5 mm; male left paramere massive basally, tip curved and hooked (Fig. 7) .... *I. elongatus* Montandon

– Ventral face of fore femur lacking prominent raised black tubercles anteriorly, although often bearing smaller brownish tubercles; smaller species, overall length clearly less than 10 mm; male left paramere not massive basally (Figs. 3, 5) 5

5. Projecting prosternal tooth attaining or exceeding distal end of second visible rostral segment; male left paramere broadened basally (Fig. 3); coloration predominantly light yellowish brown .... *I. sepikanus,* new species

– Projecting prosternal tooth reaching at most only to middle of second visible rostral segment; male left paramere slender basally (Fig. 5); coloration predominantly dark brown .... *I. isolatus,* new species

Idiocarus elongatus Montandon

Figs. 7, 12

Idiocarus elongatus Montandon, 1897:8.
Idiocarus elongatus, Lundblad, 1933:62.
Idiocarus elongatus, La Rivers, 1971:20.
Idiocarus litus La Rivers, 1971:25. **New Synonymy**.

This species, the largest in the genus, is easily recognized by its size (overall length exceeding 10.5 mm) and robust habitus, the heavily tuberculate fore femora, and the hooked tip of the male right paramere (Fig. 7). Montandon's macropterous female type came from Haveri, on the Paumomou River in southeast New Guinea, a locality we have been unable to accurately locate; specimens are at hand from drainages in the Owen Stanley Range of southeast New Guinea and the Central Highlands.

An examination of the male holotype of *Idiocarus litus* La Rivers from "PAPUA, Dogura" (probably in the vicinity of Port Moresby, Central Prov.) reveals it to be a specimen of *I. elongatus* Montandon on the basis of the male genitalia; *I. litus* is thus placed as a junior synonym of *I. elongatus.* The majority of the paratypes designated by La Rivers (1971) represent *I. papuus,* new species, and it seems likely that La Rivers intended his name *I. litus* to apply to this latter species but inadvertently selected a small specimen of *I. elongatus* as his holotype. *I. papuus* and *I. elongatus* occur sympatrically in the Central Highlands; specimens of the former species from higher elevations are often larger than those from the lowlands, however the internal male genitalic structures are diagnostic.

Material examined. PAPUA NEW GUINEA. *Central Prov.:* 7♂♂, 12♀♀, 4 nymphs, Eio Creek, nr. Baruanumu, CL 1840, 22.IX.1983; 7♂♂, 1♀, 4 nymphs, Musgrave (Aieme) River at Awarere Plantation, CL 1841, 22.IX.1983; 2♂♂, 1♀, stream nr. Musgrave River, CL 1842, 22.IX.1983; 2♂♂, 1♀, 3 nymphs, Laloki River, 15 km N of Port Moresby, CL 1845, 22.IX.1983. *Western Highlands Prov.:* 2♂♂, Baiyer River bird sanctuary, CL 1792, 8.IX.1983 (all above collected by J. T. and D. A. Polhemus, in JTP). *Province uncertain:* 1♂, Papua, Dogura, 20.VIII.1959 (E. L Cassidy) (*I. litus* holotype, CAS); 1♀, SE New Guinea, Haveri, 7.XI.1893 (Loria) (*I. elongatus* holotype, BMNH).

Idiocarus intermedius La Rivers
Figs. 4, 10

Idiocarus intermedius La Rivers, 1971:23.

This moderate sized species, described from the Star Mountains of Western Province, may be recognized by the non-tuberculate fore femora, the hair tufts at the base of the female subgenital plate (Fig. 10), the slender, curving male left paramere (Fig. 4), and the general coloration, which is pronouncedly reddish in brachypterous specimens. Though superficially similar to *I. papuus,* new species, it is morphologically distinct on the basis of pronotal structure (more massive and robust in *I. intermedius*) and genitalia. The two species are geographically sympatric, but *I. intermedius* occurs at higher elevations, and although widely distributed in the mountainous regions of the island appears to be much less common in collections. This species also appears to prefer fast current speeds, since the longest series were taken in violently rushing, cold waters.

Material examined. PAPUA NEW GUINEA. *Morobe Prov.:* 17♂♂, 9♀♀, 6 nymphs, Big Wau Creek at Wau, 1,036 m (3,400′), CL 1819, 16.IX.1983; 2♂♂, 2♀♀, 5 nymphs, Poverty Creek, Mt. Missim, 1,600 m (5,249′), CL 1830, 18.IX.1983; 1♂, 1♀, Bulolo River at Wau, 899 m (2,950′), CL 1815, 16.IX.1983; 1♂, Kauli Creek, nr. Wau, CL 1826, 17.IX.1983; 1♂, Wampit River, 10.7 km N of Mumeng on Wau road, 900 m (2,953′), CL 1833, 19.IX.1983 (all above collected by J. T. and D. A. Polhemus, in JTP). *Western Highlands Prov.:* 1♀, 1 nymph, Baiyer River, 27 km N of Mt. Hagen, CL 1792, 6.IX.1983 (J. T. and D. A. Polhemus) (JTP). *Eastern Highlands Prov.:* 2♂♂, 2♀♀, Chimbu Valley, Bismarck Range, 1,524–2,315 m (5,000–7,500′), X.1944 (P. Darlington) (CAS); 2♀♀, Goroka, 30.VI.1969 (I. La Rivers) (CAS). IRIAN JAYA: 1♀, Ok Temna, Star Range, 1,500 m, 19-V.1959, Mus. Leiden Neth. New Guinea Exp. (RNHL); 1♂, Sibil Valley, Star Range, 1,260 m, IV. 1959, Mus. Leiden Neth. New Guinea Exp. (*I. intermedius* holotype, RNHL).

Idiocarus minor La Rivers
Figs. 6, 13

Idiocarus minor La Rivers, 1971:28.

The smallest species in the genus, *I. minor* can be recognized by its diminutive size (overall length 8 mm or less), the blunt, rounded male paramere (Fig. 6), the hair tufts on the female subgenital plate (Fig. 13), and the prominent prosternal carina. This species appears to be widely distributed in the central highlands and the Owen Stanley Range, although by far the majority of specimens have come from the vicinity of the type locality at Wau. These insects prefer substrates of small diameter gravel in cold, shallow water, and have not been taken at elevations below 800 m (ca. 2,600′).

Material examined. PAPUA NEW GUINEA. *Morobe Prov.:* 1♂, Big Wau Creek at Wau, 1,036 m (3,400′), CL 1819, 16.IX.1983; 3♂♂, Poverty Creek, Mt. Missim, 1,600 m (5,249′), CL 1830, 18.IX.1983; 30♂♂, 21♀♀, Wampit River, 10.7 km N of Mumeng on Wau road, 900 m (2,950′), CL 1833, 19.IX.1983 (all above collected by J. T. and D. A. Polhemus, in JTP); 1♂, 1♀, Mt. Missim, 1,290 m (4,231′), 9.IV.1966 (G. Lippert) (paratypes, BPBM); 3♂♂, 1♀, Hospital Creek, nr. Wau, 1,143 m (3,750′), 20.X.1964 (W. G. and J. L. Peters) (LACM). *Western Highlands Prov.:* 1♂, Trauna River, nr. Baiyer River, CL 1793, 8.IX.1983 (J. T. and D. A. Polhemus) (JTP); 2♂♂, 1♀, Mt. Hagen, 1.VII.1969 (I. La Rivers) (CAS).

Idiocarus isolatus, new species
Figs. 5, 9

Description. Brachypterous form: Of small size, ovate, habitus as in Figure 1. General coloration dark brown, with scattered yellowish brown areas on head, pronotum, and abdomen. Length 8.00 mm; maximum width 3.87 mm.

Head dark brown, areas adjoining inner margins of eyes yellowish, width/length = 63/53; eyes brown, shining, inner margins straight, convergent anteriorly, separated from head by distinct furrows, these furrows deeper anteriorly, posterior/anterior interocular space = 38/28; anteclypeus well produced anteriorly into a rounded point, covering labrum, apex of head tridentate; labrum rounded, projecting far over base of rostrum; maxillary plates pointed, fuscous, projecting forward beyond anterior head margin; antennae short, yellowish brown, barely projecting beyond lateral margins of eyes; inner margins of eyes sparsely set with long erect setae; vertex well produced behind eyes, curving more sharply basally.

Pronotum dark brown, two (1 + 1) patches behind eyes to either side of midline and stripes along lateral margins yellowish brown, width/length (midline) = 133/45; lateral margins convex, mildly explanate, smooth, set with erect brown setae; posterolateral angles weakly produced, rounded; posterior margin weakly sinuate; surface minutely rugose, shining. Scutellum dark brown, shining, width/length = 93/50; lateral margins sinuate. Hemelytra brachypterous, dark brown, rugose, shining reaching to base of second abdominal tergite; lateral margins explanate, set with long gold setae.

Abdominal tergites I–VI exposed, dark brown, often marked with yellowish brown centrally and along posterior margins; lateral margins set with short stiff gold setae, sparsely set with longer golden hairs.

Ventral surface brown, darker on thorax, abdomen with a golden sheen; ventral keel of head strongly carinate, acuminate apically; prosternal plate weakly carinate medially; mesosternal plate weakly carinate medially, produced to a point distad; static sense organ ovate, gold, shining, located inside lateral pronotal margin near midpoint. Legs yellowish brown; dorsal face of fore femur anteriorly, middle and hind tibiae, infuscated; fore femur heavily set with raised dark tubercles on anterior half of dorsal face, anterior margin adjoining tibia with a fringe of short gold setae, posterior margin bearing a fringe of longer gold setae, a raised row of tubercles present on dorsal midline; fore tibia curved, slightly exceeding adjacent proximal portion of femur; fore coxae with a small row of brown tubercles running lengthwise; middle and posterior femora with two rows of tiny reddish spines running lengthwise along

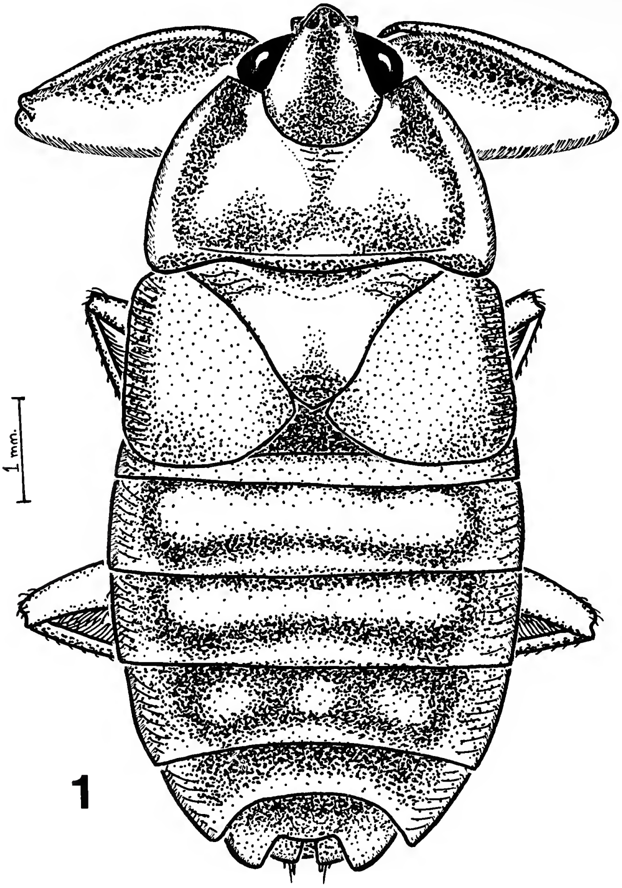


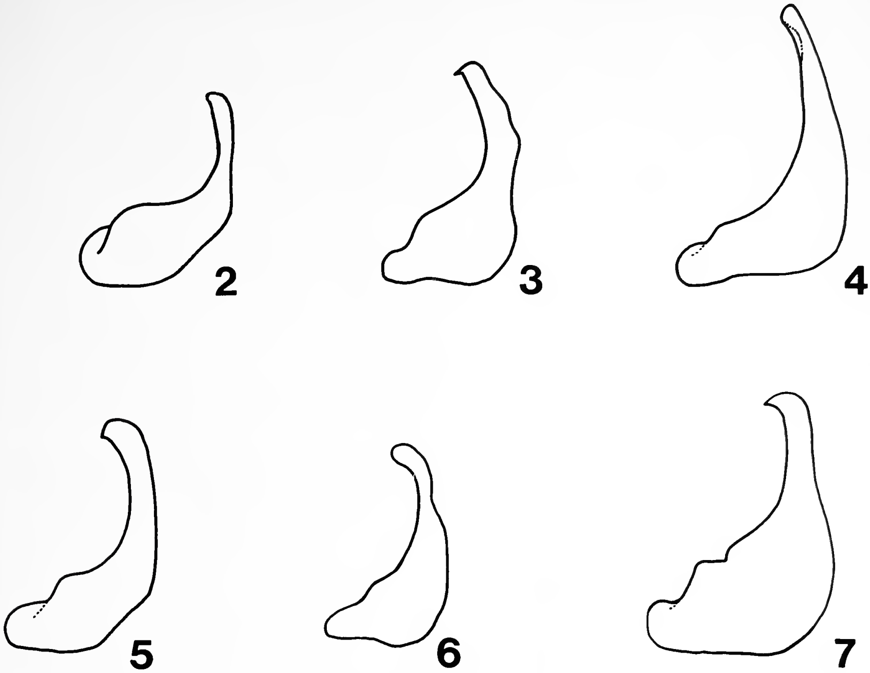
Fig. 1. *Idiocarus isolatus,* new species, brachypterous female, dorsal habitus.

posterior margins; middle and posterior tibiae set with numerous small reddish spines, five transverse rows of stout reddish spines present distally; middle and posterior femora and tibiae bearing long gold swimming hairs; claws sharply bent, yellowish brown, tips infuscated.

Male left paramere curving, weakly acuminate at tip, shape as in Figure 5; male abdominal tergite IV with a distinct indentation along posterior margin; female subgenital plate trapezoidal, tapering evenly, shape as in Figure 9.

Macropterous form: Similar to brachypterous form in size, general structure, and coloration. Wings black, reaching to abdominal tergite VI, surface rugose; clavus and embolium well delineated, membrane smooth. Scutellum enlarged, lateral margins only weakly sinuate.

Material examined. Holotype ♂, and allotype ♀: PAPUA NEW GUINEA. *Western*



Figs. 2–7. Male left parameres of *Idiocarus* species. 2. *I. papuus,* new species. 3. *I. sepikanus,* new species. 4. *I. intermedius* La Rivers. 5. *I. isolatus,* new species. 6. *I. minor* La Rivers. 7. *I. elongatus* Montandon.

Prov.: Ok Mart River at Rumginae, CL 1777, 4.IX.1983 (J. T. and D. A. Polhemus) (BPBM). Paratypes: PAPUA NEW GUINEA. *Western Prov.:* 14♂♂, 12♀♀, same data as types; 2♂♂, 2♀♀, 1 nymph, Wai Somare River nr. Ningerum, CL 1778, 4.IX.1983; 2 nymphs, 10 km S of Ningerum on Ok Tedi road, CL 1779, 4.IX.1983. *Central Prov.:* 3♂♂, 4♀♀, Eio Creek, nr. Baruanumu, CL 1840, 22.IX.1983; 5♂♂, 4♀♀, Musgrave (Aieme) River at Awarere Plantation, CL 1841, 22.IX.1983 (all above collected by J. T. and D. A. Polhemus, in JTP).

Etymology. The name “isolatus” (L., separate) refers to the remote nature of the country in which these insects occur.

Discussion. I. isolatus can be recognized by the absence of raised tubercles on the anterior venter of the fore femur, the shape of the male left paramere (Fig. 5), and the short prosternal projection, which reaches only to the middle of visible rostral segment II. Specimens at the type locality were taken from under moderate sized stones in knee deep water at the head of a riffle; none were encountered in the riffle itself or in the slack water above. All the specimens seen to date have come from the upper Fly River basin, and southward flowing drainages in the Owen Stanley Range; specimens from the latter region are somewhat larger than those from the type locality but agree in all particulars of structure, coloration, and genitalia. This species is found at lower altitudes than most other members of the genus, all the present records being from below 500 m (ca. 1,600′).

Idiocarus sepikanus, new species

Figs. 3, 11

Description. Brachypterous form: Of small size, ovate, general coloration tan with scattered brown markings. Length 7.70 mm; maximum width 3.73 mm.

Head tan, posterior margin, anteclypeus, and medially along frons and vertex, brown, width/length = 62/52; eyes brown, shining, inner margins straight, convergent anteriorly, separated from head by deep furrows set with pale erect setae, posterior/anterior interocular = 38/30; anteclypeus well produced anteriorly, covering labrum, apex of head distinctly tridentate; labrum projecting far beyond base of rostrum, apex rounded; maxillary plates projecting forward as far as apex of labrum, tan, tips fuscous; antennae short, barely exceeding lateral eye margins; vertex moderately produced behind eyes, margin evenly rounded.

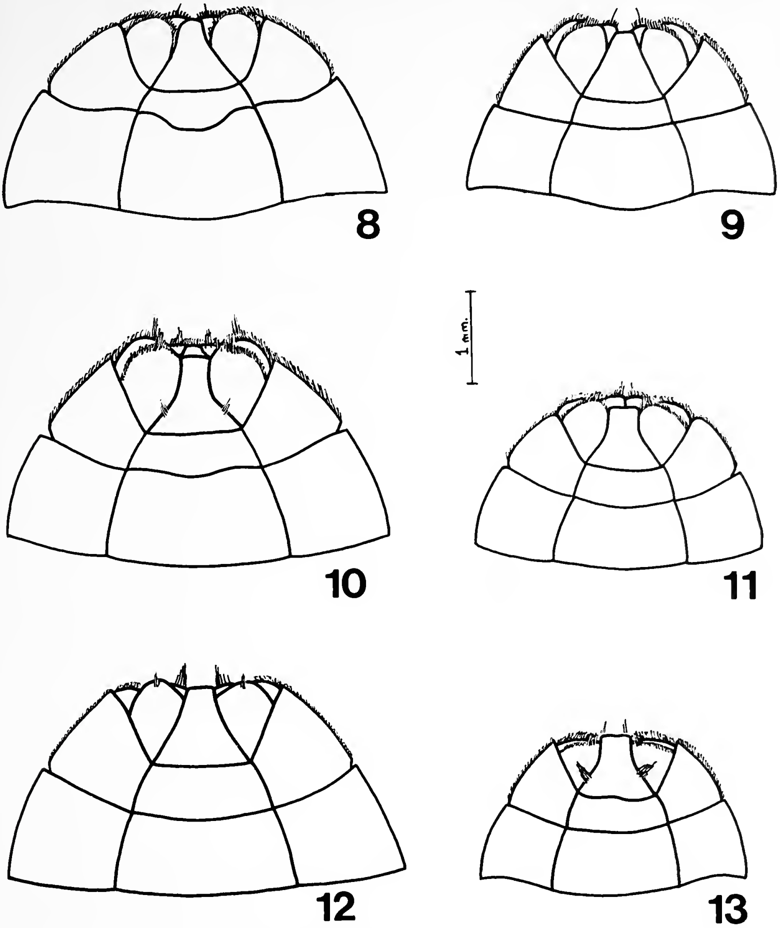
Pronotum tan, midline and areas anterolaterally adjoining eyes, brown, width/length (midline) = 130/50; lateral margins convex, smooth, posterolateral angles rounded, weakly produced; posterior areas excluding posterolateral angles frequently embrowned; surface weakly rugose. Scutellum tan, tip infuscated, surface weakly rugose, width/length = 95/45; lateral margins sinuate. Hemelytra tan, rugose, brachypterous, reaching to base of abdominal tergite II; lateral margins infuscated, explanate, sparsely set with long gold setae.

Abdomen with tergites I–VI exposed, brown, frequently tan along margins and centrally; margins bearing short stiff gold setae, interspersed with very long fine gold setae.

Ventral surface brown, prothorax darker; ventral keel of head strongly carinate, produced anteriorly into a sharp point; prosternal plate weakly carinate medially; mesosternal plate weakly carinate medially, produced into a sharp point distad; static sense organ round, gold, shining, located just inside lateral pronotal margin near midpoint. Legs pale, anterior portion of fore femur black dorsally, set with many small dark raised tubercles, portion adjoining tibia with a fringe of fine gold setae, posterior margin with a fringe of longer gold setae, a row of raised dark tubercles present along midline of ventral face; fore tibia not exceeding adjacent proximal portion of femur; fore coxa with a row of about fifteen small brown tubercles running lengthwise; middle and posterior femora with two rows of tiny brown spines running lengthwise along posterior margins; middle and posterior tibiae set with numerous small brown spines, three transverse rows of stout spines present distally; middle nd posterior tibiae and femora with long gold swimming hairs; claws sharply bent, yellowish, tips black.

Male left paramere with a sharp tooth at apex (see Fig. 3); female subgenital plate trapezoidal, narrowing markedly on posterior half (see Fig. 11).

Macropterous form: Similar to brachypterous form in size and general structure. Wings reaching to base of abdominal segment VI, dark brown; clavus and embolium well delineated, clavus and corium yellowish basally; membrane black. Scutellum enlarged, dark brown, lateral margins not sinuate.



Figs. 8–13. Female subgenital structures of *Idiocarus* species. 8. *I. papuus,* new species. 9. *I. isolatus,* new species. 10. *I. intermedius* La Rivers. 11. *I. sepikanus,* new species. 12. *I. elongatus* Montandon. 13. *I. minor* La Rivers.

Material examined. Holotype ♂, and allotype ♀: PAPUA NEW GUINEA. *East Sepik Prov.:* mountain rainforest stream near Pasam, 300 m (984′), CL 1798, 10.IX.1983 (J. T. and D. A. Polhemus) (BPBM). Paratypes: PAPUA NEW GUINEA. *East Sepik Prov.:* 14♂♂, 10♀♀, 6 nymphs, same data as types (JTP); 14♂♂, 13♀♀, 1 nymph, Nagam River, 17 mi S of Wewak, 6.VII.1969 (I. La Rivers) (CAS); 1♂, 1♀, Nagam River, 3 km S of Pasam, CL 1799, 10.IX.1983 (J. T. and D. A. Polhemus) (JTP); 3♂♂, 1♀, Yemogu Creek, 2 km W of Tring, CL 1805, 12.IX.1983 (J. T. and D. A. Polhemus) (JTP).

Etymology. The name "sepikanus" refers to the Sepik River system, in which this species occurs.

Discussion. I. sepikanus is similar to *I. minor* La Rivers with which La Rivers (1971, fig. 6) confused it. It may be recognized by the female subgenital plate (Fig. 11), the male left paramere (Fig. 3), the long prosternal projection which exceeds the tip of apparent rostral segment II, and the predominantly tan coloration of the dorsum. This species appears to be confined to the Prince Alexander Mountains and other ranges along the northern New Guinea coast. The insects prefer habitats consisting of small to moderate sized stones in shallow, flowing water, and the present records all come from streams in areas of limestone exposure.

Idiocarus papuus, new species
Figs. 2, 8

Description. Brachypterous form: Of moderate size for genus, ovate, general coloration brownish to black with scattered yellow markings. Length 9.25 mm; maximum width 4.30 mm.

Head dark brown, lengthwise patches to either side of midline adjoining eyes yellowish; width/length = 50/70; eyes brown, shining, inner margins straight, convergent anteriorly, separated from frons by distinct furrows set with pale erect setae, posterior/anterior interocular = 40/32; anteclypeus well produced anteriorly, apex tridentate; labrum well developed, brown, apex rounded; maxillary plates oriented vertically, exceeding anterior margin of head, tips pointed, infuscated; antennae slender, terminal segment exceeding lateral eye margin; vertex well produced behind eyes, posterior margin evenly rounded.

Pronotum blackish brown, areas adjoining margins and anterolaterally behind eyes yellow, width/length (midline) = 150/56; lateral margins convex, smooth, weakly explanate, posterolateral angles weakly produced, rounded; surface along midline behind vertex rugose. Scutellum brown to black, occasionally marked with yellow centrally and at anterolateral angles, width/length = 100/60, lateral margins weakly sinuate. Hemelytra brachypterous, reaching only to base of abdominal tergite II, coloration brown, lateral areas darker, set with long gold setae, overall surface weakly rugose.

Abdomen with tergites I–VI exposed, dark brown, frequently marked with yellowish along lateral and posterior margins; lateral margins fringed with short, stiff, gold setae, interspersed with longer fine gold setae.

Ventral surface brown, thorax darker; ventral keel of head sharply produced and pointed anteriorly, tip of point reaching to midpoint of second visible rostral segment; prosternal plate weakly carinate medially; mesosternal plate nearly acarinate medially, produced to a point distad; ovate gold sense organ located inside lateral prothoracic margin near midpoint; abdominal venter with fine hydrofuge pile, producing gold sheen in certain lights, depressed shining ovate sense organs present laterally on paratergites I–VI. Legs yellowish, anterior portion of fore femur black dorsally, set with small raised tubercles, margin adjoining tibia with thick fringe of short gold setae, posterior margin with thick fringe of long gold setae and row of small raised tubercles, row of raised dark tubercles present along midline of ventral face; fore coxa with a row of about 10 raised tubercles running lengthwise; middle and posterior femora with two rows of short brown spines running lengthwise along posterior margins; middle and posterior tibiae set with numerous short reddish spines, apices with five to six transverse rows of stouter spines; middle and posterior tibiae and posterior femora with long gold swimming hairs; claws sharply bent, yellow, tips infuscated.

Male left paramere slender, tip rounded (see Fig. 2); female subgenital plate tapering rather evenly, lateral margins only slightly indented, lacking basal hair tufts, apex without indentation (see Fig. 8).

Macropterous form: Similar to brachypterous form in size, general structure and coloration. Wings black, reaching to tip of abdomen; clavus, embolium and corium well delineated, surface weakly rugose; membrane smooth. Scutellum enlarged, black, shining.

Material examined. Holotype ♂, and allotype ♀: PAPUA NEW GUINEA. *Morobe Prov.:* Oomsis, 35 km SW of Lae on Wau road, 200 m (656′), in shallow rocky stream, CL 1810, 8.IX.1983 (J. T. and D. A. Polhemus) (BPBM). Paratypes: PAPUA NEW GUINEA. *Morobe Prov.:* 43♂♂, 25♀♀, 2 nymphs, same data as types; 10♂♂, 8♀♀, 4 nymphs, Perenin River along Wau road, 200 m (656′), CL 1813, 15.IX.1983; 9♂♂, 15♀♀, 3 nymphs, Poverty Creek, nr. Wau, CL 1816, 16.IX.1983; 9♂♂, 10♀♀, 4 nymphs, Wampit River, 10.7 km N of Mumeng along Wau road, 900 m (2,953′), CL 1833, 19.IX.1983; 7♂♂, 8♀♀, Crystal Creek, nr. Wau, CL 1827, 17.IX.1983; 6♂♂, 3♀♀, stream 1.5 km N of Mumeng, CL 1832, 19.IX.1983; 6♂♂, 2♀♀, stream 17.8 km N of Mumeng on Wau road, CL 1835, 19.IX.1983; 5♂♂, 2♀♀, Gurakor Creek, along Wau road, CL 1814, 15.IX.1983; 3♂♂, 3♀♀, Bamboo Creek, nr. Wau, CL 1817, 16.IX.1983; 5♀♀, 4 nymphs, Clearwater Creek, 3 km S of Mumeng, CL 1831, 19.IX.1983; 3♂♂, Clearwater Creek, nr. Wau, CL 1818, 16.IX.1983; 1♂, stream 18 km N of Lae, CL 1837, 20.IX.1983; 1♀, 2 nymphs, Bulolo River at Wau, 899 m (2,950′), CL 1815, 16.IX.1983. *Western Highlands Prov.:* 19♂♂, 26♀♀, 10 nymphs, Baiyer River, 53 km N of Mt. Hagen, CL 1783, 8.IX.1983; 10♂♂, 5♀♀, 1 nymph, Baiyer River bird sanctuary, CL 1792, 8.IX.1983; 6♂♂, 4♀♀, 1 nymph, Trauna River, nr. Baiyer River, CL 1793, 8.IX.1983; 2♂♂, 4♀♀, 2 nymphs, Walo River, 50 km N of Mt. Hagen, CL 1794, 8.IX.1983. *East Sepik Prov.:* 36♂♂, 38♀♀, 8 nymphs, Arin River, W of Wewak, CL 1803, 11.IX.1983 (all above collected by J. T. and D. A. Polhemus, in BPBM, CAS, and JTP).

Etymology. The name "papuus" refers to the island of New Guinea, to which this species is endemic.

Discussion. I. papuus is the most common species encountered in the Central Highlands of New Guinea, and may be recognized by its moderate size (length exceeding 8 mm), sinuate posterior margin of abdominal sternite V in females (see Fig. 8), and the straight arm on the male left paramere. As with other species of *Idiocarus,* considerable intraspecific variation exists in size and coloration among populations from different river systems, but the internal genital characters hold relatively constant. Individuals from the north coast ranges are smaller and lighter colored, with the upright arm of the male left paramere slightly shortened, while specimens from the central ranges tend to be larger than average and have the rounded tip of the male left paramere more highly expanded. Although these variant populations could easily be designated as subspecies, such action seems premature until the range of geographic variation within the species is more fully understood. Winged specimens of *I. papuus* may be confused with macropterous individuals of *I. inter-*

medius La Rivers on the basis of external characters, although the former species has a generally broader and more robust overall habitus and lacks tubercles on the dorsum of the fore femur; dissection of the male genitalia is often necessary for definitive identification of specimens from the same locality. La Rivers' paratype series of *I. litus* from "Wau Valley, Bulolo River" is actually composed of specimens of *I. papuus*; the same holds true for the majority of other specimens of the now synonymized *I. litus* held in collections.

This species prefers shallow water riffles, where it is often found in large numbers amid small stones and coarse gravels. In larger rivers the insects occur in shallow rocky areas near shore, and rarely out in the deeper sections of the stream. The type locality at Oomsis, lying in low foothills behind the coast at an elevation of only 200 m (656 feet) is one of the lowest localities at which *Idiocarus* have been taken.

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Received February 27, 1985; accepted June 17, 1985.

J. New York Entomol. Soc. 94(1):51–55, 1986

ORTHOCEPHALUS SALTATOR HAHN (HETEROPTERA: MIRIDAE): CORRECTIONS OF MISIDENTIFICATIONS AND THE FIRST AUTHENTIC REPORT FOR NORTH AMERICA

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Abstract. —The first authentic report is given for the halticine plant bug, *Orthocephalus saltator* (Hahn) (Heteroptera: Miridae), in North America from Canada: New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and the United States: New York, Pennsylvania, and Virginia. Male parameres are illustrated and diagnoses are provided to help separate *O. saltator* from the holarctic *Orthocephalus coriaceus* (Fabricius). Previous records of *O. saltator* from Alaska are considered misidentifications of *Irbisia sericans* Stal.

While working on undetermined Miridae, we discovered a halticine mirid from Eastern North America that belongs in the genus *Orthocephalus* Fieber. These specimens have yellow tibiae and are more slender and uniformly black than the holarctic *Orthocephalus coriaceus* (Fabricius), known from the northeastern United States (Wheeler, 1985). By using Wagner's (1973) key to the Mediterranean species of *Orthocephalus,* we were able to identify these specimens as *O. saltator* (Hahn). Confirmation was made by comparing our material to European specimens of *O. saltator* housed in the U.S. National Museum of Natural History (USNM).

In this paper, we give the first authentic records of *O. saltator* for North America, redescribe the adult of *O. saltator,* figure male parameres of *O. coriaceus* and *O. saltator,* provide diagnoses to separate these two species, and correct the misidentifications of *O. saltator* in the North American literature.

Orthocephalus saltator ranges throughout Europe to eastern Siberia (Carvalho, 1959; Kulik, 1965). In North America, *O. saltator* has been incorrectly recorded from Alaska (Uhler, 1886; Schwarz, 1899; McAtee, 1923) and Canada (Provancher, 1872). Recorded hosts include: *Chrysanthemum, Ononis, Thymus serphyllum* L., *Trifolium,* and *Vicia cracca* L. (Butler, 1923); *Cichorium, Hieracium* and other composites [Asteraceae] (Kerzhner, 1964); and *Hieracium pilosella* L. (Wagner, 1973).

CORRECTIONS OF MISIDENTIFICATIONS

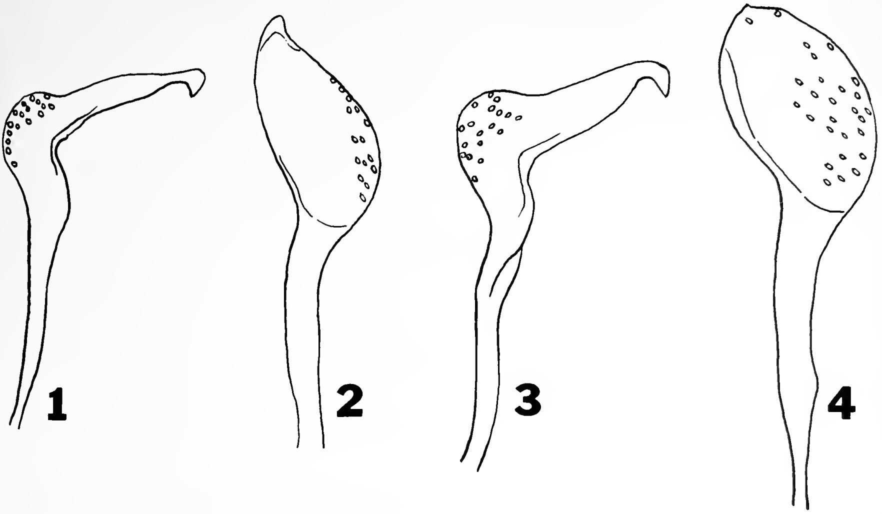
Pribilof Islands records. The most persistent record of *O. saltator* from North America was given by Schwarz (1899) (and repeated by McAtee, 1923) based on a brachypterous specimen collected on St. Paul Island (Pribilof Island group) about 180 miles north of the Aleutian Island chain, Alaska. Perusal of the USNM collection, however, did not reveal any specimens identified a *O. saltator* from Alaska or any of its coastal islands, including the Pribilofs. Finally, in reading a reprint of the original report, we noticed that Heidemann (handwriting identified by R. C. Froeschner, Department of Entomology, USNM) had annotated the *O. saltator* record in the USNM copy as *Irbisia sericans* Stål, suggesting that he had seen the Schwarz specimen. Further, Heidemann (1900) reported a large number of *I. sericans* from the Pribilofs, but did not refer to Schwarz's paper, apparently because both papers were in press at the same time. The USNM collection contains most of the *I. sericans* reported by Heidemann (all confirmed by M. D. Schwartz in preparation for his excellent revision of the genus *Irbisia* Reuter [1984]). Also there is a single brachypterous female of *I. sericans* in the collection labeled "Pribilof Isl., ♀" that could be the specimen Schwarz reported (also confirmed by Schwartz). Considering that *I. sericans* and *O. saltator* are both black, have silvery pubescence and yellow tibiae, and brachypterous forms are common, it is not surprising that Schwarz confused the two species, even though *I. sericans* belongs in the subfamily Mirinae and *O. saltator,* in the Orthotylinae. Based on the overall similarity of the two species and the subsequent identification of the USNM specimens, it appears certain that the *O. saltator* record from the Pribilof Island should be applied to *I. sericans.*

Other misidentifications. Uhler (1886) in his Checklist recorded *O. saltator* from Sitka [Alaska]. This record has appeared in a number of other papers, including Reuter (1891), Van Duzee (1917), and Slater and Baranowski (1978). There is a single specimen in the USNM collection from Sitka that is determined by Uhler as *O. saltator*; it is *I. sericans* (identity confirmed by Schwartz; *I. sericans* was described from Sitka, Alaska [see Schwartz, 1984]).

The only apparent Canadian record [no locality given] for *O. saltator* was reported by Provancher (1887). In studying the Provancher collection, Van Duzee (1912) indicated that Provancher's specimen(s) was not recognizable to genus but clearly was not *O. saltator.* Knight (1917) stated that he had not seen any material of *O. saltator* from North America, but that Provancher's (1889) description fit very well. Later, he (Knight, 1920) suggested that the record probably referred to a species of *Irbisia* or, possibly in part, to *Orthocephalus mutabilus* (Fallén) [a junior synonym of *O. coriaceus* (Fabricius)]. We have been unable to find Provancher material in the collection at the University of Laval, Quebec, but because Van Duzee did see the specimens and dismissed them as not representing *O. saltator,* we consider Provancher's record of the species for North America in error.

FIRST NORTH AMERICAN RECORDS

Our combined data for *O. saltator* in North America, including records supplied by A. G. Wheeler, Jr. (Pennsylvania Department of Agriculture, Harrisburg [PDA]), are: NEW BRUNSWICK.—1 macropterous (M) male, 3 brachypterous (B) females, Fundy Nat. Park, July 6, 1966, L. A. Kelton (CNC); 1 M male, Kouchiboguac Nat. Park, Aug. 21, 1978, L. B. Lyons (CNC). NEW YORK.—2 M males, Tompkins Co., Ithaca, Snyder Heights, June 27, 1978, J. G. Franclemont and E. R. Hoebeke coll. (Cornell Univ., USNM); 1 M male, Tompkins Co., Ithaca, July 3, 1974 [no coll. data] (Cornell Univ.); numerous adults (all wing forms) and nymphs, Tompkins Co., 2 mi S Trumansburg, June 24–28, 1985, E. R. Hoebeke coll., taken on spotted knapweed, *Centaurea maculosa* Lam. and chicory, *Cichorium intybus* L. (Cornell



Figs. 1–4. Male parameres of *Orthocephalus* spp. *O. saltator*: 1. Left paramere. 2. Right paramere. *O. coriaceus*: 3. Left paramere. 4. Right paramere.

Univ.); 1 B female, Onondaga Co., Elbridge–Camillus line, June 26, 1982, A. G. Wheeler, Jr. coll., taken on *Cichorium intybus* (PDA); 1 B female, Monroe Co., Egypt, July 31, 1982, A. G. Wheeler, Jr. coll., taken sweeping (PDA); 1 M female, Watkins Glen, Schuyler Co., June 28, 1985, E. R. Hoebeke coll., taken on *Cichorium intybus* (Cornell Univ.). NOVA SCOTIA.—2 M males, Berwick, July 7, 1947, Schultz and Brown (CNC); 3 M males, Kentville, July 15, 1966, L. A. Kelton (CNC); 3 M males, 1 B female, Mt. Uniacke, July 13–14, 1966, L. A. Kelton (CNC); 3 M males, 1 M female, 2 B females, St. Joseph Du Moine, July 23, 1966, L. A. Kelton (CNC). ONTARIO.—2 B females, Waterford, July 17, 1962, Kelton and Thorpe (CNC). Prince Edward Island.—1 B female, Cavendish Nat. Park, July 9, 1966, L. A. Kelton (CNC); 1 B female, Borden, Aug. 6, 1966, L. A. Kelton (CNC); 1 B female, Rustico, Aug. 4, 1966, L. A. Kelton (CNC). PENNSYLVANIA.—1 B female, Juniata Co., Richfield, July 13, 1982, A. G. Wheeler, Jr. coll., taken on *Cichorium intybus* (PDA); 1 M male, Susquehana Co., Thompson, June 28, 1985, A. G. Wheeler, Jr. coll., taken on *Cichorium intybus* (PDA); 1 M male, 1 B female, Wyoming Co., Tunkhannock, June 28, 1985, A. G. Wheeler, Jr. coll., taken on *Cichorium intybus* (PDA). VIRGINIA.—3 B females, Rockingham Co., Harrisonburg, June 9, 1982, A. G. Wheeler, Jr. coll., taken on *Cichorium intybus* (2 PDA, 1 USNM); 8 M males, 4 B females, Rockingham Co., Harrisonburg, May 25, 1985, T. J. Henry and A. G. Wheeler, Jr., taken on *Cichorium intybus* (USNM); 1 M female, Woodstock, Rt. 81, Shenandoah Co., May 25, 1985, T. J. Henry and A. G. Wheeler, Jr., taken on *Cichorium intybus* (USNM).

These are the first correctly identified specimens, constituting a considerable range extension for this widespread western palearctic species. Because the known distribution of *O. saltator* in Eastern North America is nearly as great as that known for

O. coriaceus (Wheeler, 1985) and our earliest collection date is 1947, it seems likely that it was introduced on plant material near the time or not long after *O. coriaceus* (Knight, 1917). Its close similarity to *O. coriaceus* probably accounts for it being overlooked until now.

TAXONOMY

Description. Macropterous male: Length 5.75–6.33 mm, width 1.88–2.04 mm; overall coloration of body uniformly, shiny black; dorsum and undersurface thickly set with silvery, flattened, scale-like pubescence, dorsum with long, black, bristle-like, simple setae. Head: Width 1.08–1.12 mm, vertex 0.52–0.54 mm. Rostrum: Length 1.36–1.42 mm, extending to bases of mesocoxae. Antennae: Uniformly black, thickly pubescent, with some setae subequal to or longer than diameter of segments; segment I length 0.44–0.46 mm, II 1.40–1.48 mm, III 1.00–1.12 mm, IV 0.52–0.54 mm. Pronotum: Length 0.72–0.80 mm. Hemelytra: Uniformly black; membrane and veins dark brown or fuscous. Legs: Femora tarsi, and claws black, tibiae yellow, sometimes black at bases and apices. Genitalia: Left paramere (Fig. 1); right paramere (Fig. 2).

Macropterous female: Similar to macropterous male in color and general size, but slightly broader with the wing membrane more abbreviated.

Brachypterous female: Appearing much smaller than macropterous forms because of the much abbreviated, coleopteriform hemelytra; membrane absent. Length to apex of abdomen 3.56–4.00 mm, length to apex of hemelytra 3.24–3.76 mm. Tibiae yellow as in males, although two specimens have the metatibiae black.

Remarks. The genus *Orthocephalus* can be keyed in Knight (1923, 1941) or Slater and Baranowski (1978). Species of the genus are recognized by the convergent parempodia and the shiny black body possessing black bristle-like setae, intermixed with silvery, flattened, scale-like pubescence.

Orthocephalus saltator is easily separated from *O. coriaceus* by the larger size, more slender form, uniformly black hemelytra, yellow tibiae, and the male parameres (Figs. 1, 2), especially in the more slender right paramere (Fig. 2). *O. coriaceus* is much shorter (macropters measure 4.75–5.00 mm long), the outer area of the clavus and inner area of the corium are pale in macropters, the tibiae are uniformly black, and the male parameres are slightly larger (Figs. 3, 4), especially the broader right paramere (Fig. 4). Brachypterous males and females of *O. saltator* are best separated by the yellow tibiae and more slender form.

ACKNOWLEDGMENTS

We thank E. R. Hoebeke (Cornell University, Ithaca, New York) for lending specimens and A. G. Wheeler, Jr. (Pennsylvania Department of Agriculture, Harrisburg) for lending specimens and reviewing the manuscript. We also thank J. M. Perron (Department of Biologie, University of Laval, Quebec) for searching the Provancher Collection for the specimen(s) labeled *Orthocephalus saltator.*

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Received May 10, 1985; accepted June 17, 1985.

J. New York Entomol. Soc. 94(1):56–61, 1986

AN ADVENTIVE SPECIES OF *BRACHYDEUTERA* LOEW IN NORTH AMERICA (DIPTERA: EPHYDRIDAE)

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Abstract.—*Brachydeutera longipes* Hendel, a species previously known from the Orient, is reported to occur in eastern North America (Maryland south to Georgia). This is the 4th species of *Brachydeutera* for North America and the only adventive one in recent times. The natural history of the species, mostly based on published records from India, keys, a description, and illustrations are provided to facilitate identification and future research on the species.

Publication of systematic studies frequently prompts additional research on the same taxa. Such was the beginning of the research reported here. Soon after revising the species of *Brachydeutera* from the Oriental, Australian, and oceanian regions (Mathis and Ghorpade, 1985) and publication of a smaller paper on North American species of the same genus (Mathis, 1983), one of us (WES) collected several specimens of a pale-colored congener from Georgia. Even without dissections, usually a requisite for species identification in this genus, the species was recognized as being new to North America. Unfortunately the specimens were females, which have not been studied as well and are not identifiable in some cases. Rummaging through newly collected material from Maryland, we then found additional females of what was apparently the same, pale-colored species, and on a subsequent field trip to North Carolina, WES succeeded in collecting a long series of both males and females of the same species. All specimens from the various localities were attracted to and collected at black lights in the early evening.

Unlike other species from the Western Hemisphere, these specimens are pale colored, especially the mesonotum, and the usual sharp demarcation between dark and pale coloration in the notopleural region is lacking. With careful study of the males from North Carolina, including dissection of their terminalia, this species proved to be *B. longipes* Hendel, a species known previously from the Orient. In this paper we report the occurrence, apparently adventive, of *B. longipes* in North America. Also provided is a key to North American species of *Brachydeutera,* a description and figures of *B. longipes* to facilitate its identification, and information on the natural history of the species.

KEY TO NORTH AMERICAN SPECIES OF *Brachydeutera* LOEW

1. Brown color of mesonotum gradually becoming paler laterally, merging with pale gray pleural coloration (Maryland south to Georgia) .... *B. longipes* Hendel
– Brown color of mesonotum continued ventrally to about dorsal ⅙–⅓ of anepisternum, thereafter sharply delimited from pale gray coloration of ventral pleural areas 2
2. Facial carina low, bluntly rounded, especially ventrally; male terminalia with epan-

drium, in lateral view, evenly rounded, digitiform, in posterior view, narrowly rounded, not truncate; extended arm of gonite angulate, apex narrowly pointed (Texas to California, south into Mexico) .... *B. sturtevanti* Wirth

– Facial carina high, sharply defined, especially ventrally 3

3\. Merger of fused surstyli with epandrium, in lateral view, indicated by an angulate emargination; gonite spatulate apically (Florida to Texas, southward throughout most of the neotropics) .... *B. neotropica* Wirth

– Merger of fused surstyli with epandrium, in lateral view, broadly rounded; gonite digitiform apically, narrowly rounded (eastern North America; Michigan to Maine, south to Texas and Florida) .... *B. argentata* (Walker)

Brachydeutera longipes Hendel

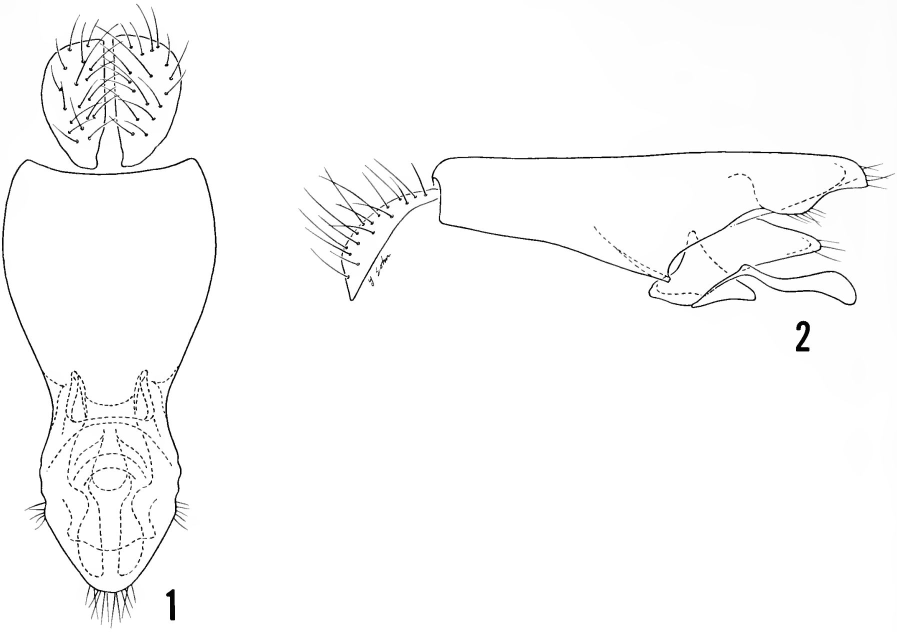
Figs. 1–3

Brachydeutera longipes Hendel, 1913:99. Wirth, 1964:7 [revision]; Ramachandra Rao, 1970:354; Cogan and Wirth, 1977:337 [Oriental catalog]; Mathis and Ghorpade, 1985:15–18 [revision].

Diagnosis. Moderately small to medium-sized shore flies, length 2.10 to 3.15 mm. Head: Frons mostly grayish brown to light brown, with faint olivaceous areas posterolaterad of ocelli; prominent, lateroclinate fronto-orbital bristles 3, anterior bristle weaker, about ½ length of posterior 2. Antenna brown, darker than frons; aristal branches 8–9. Facial carina wide, low, and rounded, weakly developed between antennae. Face, clypeus, and gena concolorous, pearly gray, facial carina and antennal fovea slightly darker, lightly tinged with faint olivaceous to grayish blue, extreme dorsum of facial carina sometimes faintly brownish. Palpus pale, yellowish.

Thorax: Mesonotal chaetotaxy comparatively poorly developed; bristles inconspicuous, setae of main setal tracks small. Mesonotum light brown to olivaceous gray, concolorous with frons, sometimes with darker brown stripes through setal tracks and with areas laterad of setal tracks more olivaceous gray, postpronotum and dorsum of scutellum mostly grayish. Scutellar ratio 0.85; apical bristles approximate, distance between them less than that between basolateral scutellar bristle and apical one. Anterior notopleural bristle present, although weaker than posterior one; katepisternal bristle present but very inconspicuous, pale, whitish. Light brownish coloration of mesonotum gradually merged with grayish coloration of pleural areas, notopleuron mostly light brownish, coloration sometimes extends to dorsolateral portions of anepisternum. Femora and tibiae yellowish, forefemur lacking sparsely microtomentose area anterodorsally toward base; tarsomeres brown to dark brown apically; male hindtibia lacking patch of ventral, long setae. Wing hyaline, clear; R_{2+3} moderately arched; R_{4+5} very slightly arched, nearly straight; costal vein ratio 3.10; M vein ratio 0.51.

Abdomen: Dorsum light brown anteriorly and medially, otherwise mostly gray; moderately microtomentose, mostly dull. Male terminalia (Figs. 1, 2) as follows: dorsal surface of epandrium in posterior view shallowly concave; epandrial width at dorsum extended laterally slightly beyond lateral margins of cerci; lateral margins of epandrium sinuate and more narrowed ventrally; epandrium + surstyli with lateral margins directed inward, apex narrowly rounded, broadly v-shaped, in lateral view



Figs. 1, 2. *Brachydeutera longipes*: 1. Cerci and epandrium (plus fused surstyli ?), posterior view. 2. Cerci, epandrium, and gonite, lateral view.

with anteroventral angle sharp, thereafter more or less evenly curved to epandrial connection except for a broad, bluntly rounded, setose process; gonite generally narrow, slightly enlarged apically, spatulate.

Specimens examined from the Nearctic Region. GEORGIA: Tattnall Co., Reidsville, Gordonia-Alatamaha State Park (at black light), Nov. 10, 1983, W. E. Steiner, A. G. Gerberich, and J. E. Lowry (12♀♀; USNM). MARYLAND: Montgomery Co., Silver Spring (at black light), July 31, 1984, W. E. Steiner and J. E. Lowry (1♀; USNM). Talbot Co., Wittman (at black light near open fields, mixed forest and tidal creek), Aug. 11–12, 1984, W. E. Steiner (5♀♀; USNM). NORTH CAROLINA: Columbus Co., Lake Waccamaw (at black light in sandy oak and pine forest near lake), Oct. 27–28, 1984, W. E. Steiner and A. G. Gerberich (36♂♂, 16♀♀; USNM).

Distribution. Iraq to Japan, south to Sri Lanka and Indonesia; eastern U.S. (Fig. 3) from Maryland to Georgia. This is the most widespread species of *Brachydeutera* in the Orient. Its distribution also extends northward into the eastern Palaearctic Region (Japan: Kyoto). The locality from Iraq was not located on a map and is unconfirmed. The occurrence of this species in eastern North America apparently is an introduction. We suspect that eggs or immatures accompanied shipment of aquatic plant material to the U.S.

Natural history. In a series of papers, Venkatesh et al. (Venkatesh is the first author with different sets of coauthors; 1975, 1976, 1977, 1977, 1978, 1981) has reported

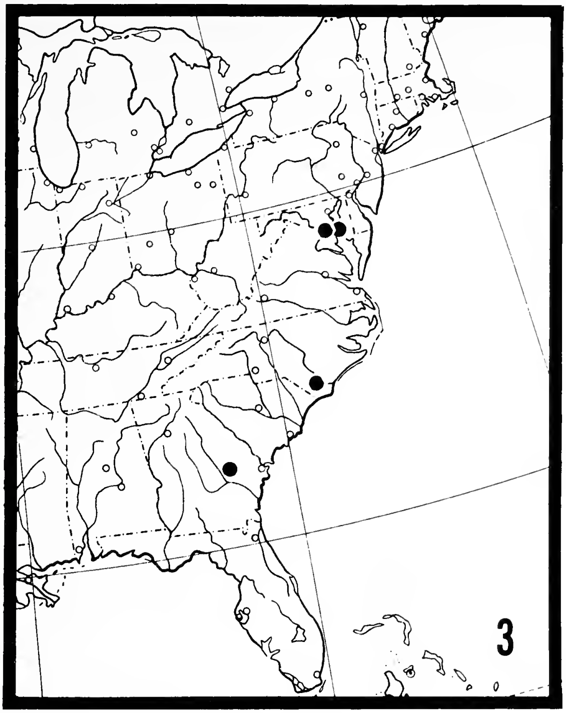


Fig. 3. Distribution map of *Brachydeutera longipes.*

on the feeding habits, behavior, and population ecology of *Brachydeutera longipes.* The summary here is largely extracted from their publications.

In India *B. longipes* is multivoltine. Gravid females oviposit on the water's surface or on moist substrates, and the developmental period, oviposition to adult, is from six to 20 days (egg 0.5–3 days; 1st instar larva 1–2 days; 2nd instar larva 1–4 days; 3rd instar larva 2–7 days; puparium 1–8 days), depending on temperature and humidity. Based on rearing experiments in the laboratory, length of the developmental period was found to be positively correlated with humidity but negatively correlated with temperature. Hence climatic and seasonal variation can greatly influence the rate of growth.

Although this species occurs in most aquatic or semiaquatic habitats, it is more abundant in relatively stable sites, those with permanent water sources, and where there is also considerable pollution and aquatic weeds. In rural India the fly was most abundant around open sewage; in urban areas the fly bred best in association with septic tanks. Along with *Tubifex* worms, the occurrence of larvae of *B. longipes* is used as an indicator of pollution in India.

The larvae *B. longipes* are epipelagic swimmers and feeders, and trophically there is some overlap and competition with larvae of the mosquito *Culex quinquefasciatus*

Say (as *C. fatigans* in most of the papers). Gut analysis revealed that larvae of *B. longipes* eat species of several genera of algae (*Chlamydomonas, Chlorella, Euglena, Scenedesmus,* and *Clathrocystis*) and some species of protozoan ciliates (*Frontonia* and *Tetrahymena*).

Adults of this species are attracted to lights, especially black lights. Many of the specimens we examined from the Oriental Region, were collected at light traps that were set out to sample mosquitoes. *Setacera* Cresson is the only other shore fly genus that we are aware of that is attracted to lights.

Remarks. The species can be distinguished by its lighter coloration, especially of the mesonotum, and by the presence of an anterior notopleural bristle. The anterior notopleural bristle is weaker than the posterior one but is still quite conspicuous. To distinguish *B. longipes* from *B. pleuralis* it is best to use characters of the male terminalia and perhaps the scutellar ratio.

ACKNOWLEDGMENTS

Special thanks are extended to Hollis B. Williams and Paul J. Spangler for reviewing a draft of this paper. Young Sohn carefully prepared the illustrations. We thank Andrew G. Gerberich and J. Elaine Lowry for assistance in collecting specimens.

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Received March 28, 1985; accepted June 18, 1985.

J. New York Entomol. Soc. 94(1):62–69, 1986

FOUR NEW SPECIES, TWO EACH OF *ATHLOPHORUS* AND *MACROPHYA* (HYMENOPTERA: TENTHREDINIDAE) FROM INDIA

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Abstract.—Four new species of Tenthredinidae, i.e., *Athlophorus vespiformis* and *A. bandatus* belonging to the Selandriinae (according to Malaise's classification) and *Macrophya gopeshwari* and *M. concolor* belonging to Tenthredininae are reported from India.

This is the third report in the series of papers dealing with new records of Symphyta from India. In it are described four new species, two each belonging to *Athlophorus* Burmeister (Selandriinae) and *Macrophya* Dahlbom (Tenthredininae). With this, the total number of so far described *Athlophorus* species comes to seven and of *Macrophya* to nine, from India. Since Cameron (1899), Rohwer (1912, 1916, 1921), Forsius (1930) and the comprehensive reviews by Malaise (1945, 1947) no new additions have been made to the list of Indian *Athlophorus* and only one to *Macrophya* by Muche (1983). All holotypes are deposited in the F.R.I., Dehradun, U.P. India.

Athlophorus vespiformis, new species

Description. Female: Length, 10.6 mm. Body fulvous to brown, with the following areas dark brown to black: antennal segments 6–9 and tip of 5th, middle fovea, areas surrounding supraclypeal pits, spot lateral to each posterior ocellus, spot on lower hind orbit, irregular large spot on lateral side of pronotum, triangular spot on mesonotal middle lobe, two spots on each lateral mesonotal lobe, posterior one-third of propleuron, irregular large spot on mesoepimeron, anteroventral border of episternum, mesosternum, entire metapostnotum, most of metapleuron and metasternum, lateral spots on first abdominal segment, proximal ⅖ of abdominal terga 2–4 and 7–8, 5–6 entirely, abdominal sternites 4–6 and metacoxae; yellowish as follows: mouthparts, clypeus, a narrow stripe along inner and outer margins of eye, narrow anterior margin and spot on posteroventral margin of pronotum, two lateral spots on scutellum, spot on raised part of mesopleuron, posterodorsal border of meso- and metepimera, lateral spots on metanotum, distal border of abdominal segments 1–4 and 7–8. Wings hyaline. Forewing with deeply infuscated radial cell (Fig. 4), veins brown to black.

Clypeus semicircularly incised (⅓ depth of its mesial length) with distinct lateral teeth and with a transverse carina along its distal margin, labrum flat with roundly pointed anterior margin, malar space equal to diameter of an ocellus, inner margin of eyes slightly emarginate, lower interocular distance equal to eye length, ratio of distances from posterior ocellus to eye, between posterior ocelli and from posterior ocellus to hind margin of head, 0.75:0.25:1.0. Antenna 2× head width, 1st and 2nd antennal segments each longer than broad, 3rd and 4th in ratio 6:5 (Fig. 8), 4–9 decreasing in length, antenna incrassate in middle. Frontal area raised to level of eyes, postocellar furrows sharp, postocellar area longer than broad in the ratio of 5:4, head carinate behind eyes.

Head with very fine and dense punctures, punctures less dense and minute on lower hind orbits. Frontal area with large and confluent punctures. Pronotum and mesonotal middle lobe densely and minutely punctured, lateral lobes with deep and dense punctures, scutellum with deep scattered punctures, appendage impunctate. Mesopleuron with large deep and dense punctures. Mesoepimeron and metaepimeron almost impunctate, mesosternum and metasternum finely punctured. Abdominal segments 1–3 impunctate, 4–9 minutely and uniformly punctured. Body covered with golden pubescence. Female lancet (Fig. 10).

Male: Length 9.8 mm, otherwise similar in all respects to female. Male genitalia (Figs. 12, 17).

Material examined. Holotype ♀, 20.6.83, collected from Mandal area (U.P.), India, 7,200 feet. Paratypes: 20♀♀, 12♂♂ with same data as the holotype.

Etymology. The name is based on its close resemblance with wasps.

Remarks. This species does not key past couplet 4 in Malaise's key (1947). This key can be modified as follows to insert this species:

4. The infuscation of the front wings prolonged in a mostly straight oblique line basal to stigma on both sides of subcosta, but decreasing in width and strength towards the base of the wing and may thus easily be overlooked basal to stigma (Plate I, B). Propodeum uniformly dull owing to minute and very dense punctures, only the extremely narrow (filiform) hind margin may be impunctate and shining. Postocellar area longer than it is wide, as 5:3; the lateral furrows faintly curved and rather sharp but not deep, and reaching little more than half way to the hypothetical hind margin of the head, but prolonged to it by distinct but very narrow, stripe-like seams. Frontal area ill-defined and likewise the antennal furrows lateral to it. Interantennal furrow deep and sharp. Antennae as long as head, thorax, and propodeum combined; the 3rd joint longer than the 4th one and the maximal width of the 6th and 5th joints subequal. Mesopleura with large scattered punctures, the surface between these with some scattered and very minute punctures, more or less shining. Abdomen strongly contracted behind the base. Hind basitarsus longer than the following tarsal joints combined. Length ♂ 10–10.5 mm; ♀ 11–12 mm 5

– Infuscation of the front wings not reaching basal to stigma 4a

4a. Head distinctly shining above, impunctate or with ill-defined punctures behind the eyes and ocelli 7

– Head with fine and dense punctures. Forewings hyaline except radial cell infuscated. Clypeus semicircularly incised with acute lateral teeth. Antenna incrassate in the middle and segments 3 and 4 in the ratio 6:5. Frontal area raised to level of eyes. Head carinate behind eyes. Mandal (U.P.), India 7,200 feet .... *Athlophorus vespiformis*, new species

5. Postocellar area and temples . . .

Athlophorus bandatus, new species

Description. Male: Length, 9.8 mm. Body black, with yellowish areas as follows: labrum, bases of mandibles, palpi, angles of clypeus, very narrow margin of inner orbits, distal ⅔ of 2nd abdominal segment, a triangular stripe along proximal margin of 4th segment, sternites 2–4 entirely, distal ends of all coxae, trochanters, and four front legs anteriorly; brownish black as follows: entire mesoleg posteriorly except yellowish proximal half of femur, distal ⅘ of metatibia and entire tarsus. Wings hyaline. Forewing with a spot below stigma (Fig. 3), veins and stigma fulvous.

Clypeus semicircularly to squarely incised (⅓ depth of its medial length) with horizontal transverse carina along distal margin, labrum flat with roundly pointed anterior margin, malar space half diameter of ocellus. Inner margins of eyes slightly converging, lower interocular distance equal to eye breadth, ratio of distances from posterior ocellus to eye, between posterior ocelli and from posterior ocellus to hind margin of head 0.75:0.25:0.65. Antenna 2½× head width, segments 1 and 2 each longer than broad, 3 as long as 4 (Fig. 7), 5–9 slightly compressed and decreasing in length. Frontal area depressed below level of eyes, postocellar furrows distinct, postocellar area as long as broad with distinct longitudinal middle carina; head carinate and narrowing behind eyes; scutellum pyramidally elevated.

Head finely and uniformly punctured, the distance between punctures almost equal to diameter of each puncture. Lower corners of pronotum and middle mesonotal lobe punctured similar to head. Mesonotal lateral lobes and scutellum with more dense and large punctures. Postscutellum with punctures similar to those of mesonotum. Elevation of mesopleuron densely and deeply punctured. Meso- and metasternum and metapleuron minutely punctured, metapostnotum and abdominal segments almost impunctate. Body covered with white pubescence. Male genitalia (Figs. 14, 18).

Female: Unknown.

Material examined: Holotype ♂, 20.6.83, collected from Mandal area (U.P.), India, 7,200 feet. Paratype: 1♂ with same data as holotype.

Etymology. The name is based on the prominent band on the abdomen.

Remarks. This species does not key past couplet 1 in Malaise's key (1947). The key can be modified as follows to key out this species:

1. Front wings with a strongly infuscated spot 1a
– Wings faintly hyaline, almost clear, and without infuscated spot in the radial cells. Antennae slender 2
1a. Front wing with a strongly infuscated spot covering basal half of radial cell. Body including antenna black, anterior side of four front legs yellowish, clypeus semicircularly to squarely incised. Malar space half diameter of ocellus, inner margins of eyes slightly converging. Antenna slightly compressed and equal to 2½× head width, antennal segment 3 as long as 4. Frontal area depressed below level of eyes. Head not carinate. Mandal (U.P.), India, 7,200 feet .... *Athlophorus bandatus*, new species
– Front wings with a strongly infuscated spot, covering most of the radial cells 3

Macrophya gopeshwari, new species

Description. Male: Length 9.2 mm. Antenna and head black, yellowish white as follows: palpi, proximal half of mandibles, labrum, irregular spots on lower inner and outer orbits, a triangular spot on middle fovea and two lateral spots on postocellar area. Thorax black, yellowish white as follows: posterior and posteroventral margins of pronotum, proximal ⅔ of tegulae, a V-shaped mark on posterior tip of mesonotal middle lobe, anterior slope of scutellum, irregular spot on anterior aspect of mesopleuron, posterodorsal angles of mesoepimeron. Abdomen brownish black except two yellowish spots on lateral side of first two segments. Legs yellowish white, black as follows: posterior side of four front legs up to middle of femur (irregular spots on outer sides of coxae), distal ⅖ of metafemur, entire metatibia, apical ⅔ of last tarsal segments and all basitarsi except their extreme tips. Forewing hyaline with apex weakly infumate (Fig. 2), veins and stigma brownish black.

Clypeus semicircularly incised (⅕ depth of its medial length), labrum flat with narrowly rounded anterior margin. Malar space almost equal to diameter of an ocellus, inner margins of eyes slightly emarginate and converging downward, lower interocular distance equal to eye length, ratio of distances from posterior ocellus to eye, between posterior ocelli, and from posterior ocellus to hind margin of head, 0.75:0.25:0.50. Antenna 3× the head width, incrassate in middle, strongly compressed, tapering towards apex, two basal segments as long as broad, segment 3 and 4 in ratio 6:5 (Fig. 6). Supraclypeal pits distinct, frontal area ill-defined and depressed below level of eyes, postocellar furrows weak, postocellar area as long as broad. Head carinate and strongly converging behind eyes.

Head with minute, scattered punctures, mesonotum with dense and small punctures and the distance between punctures equal to ½ diameter of a puncture, anterior slope of scutellum with slightly larger punctures, appendage and postscutellum densely punctured, mesopleuron distinctly punctured, punctures on mesosternum similar to that of mesonotum, metapleuron and metasternum finely punctured. Abdomen minutely punctured except impunctate stripes along posterior borders of all terga. Body covered with silvery pubescence. Male genitalia (Figs. 13, 16).

Female: Unknown.

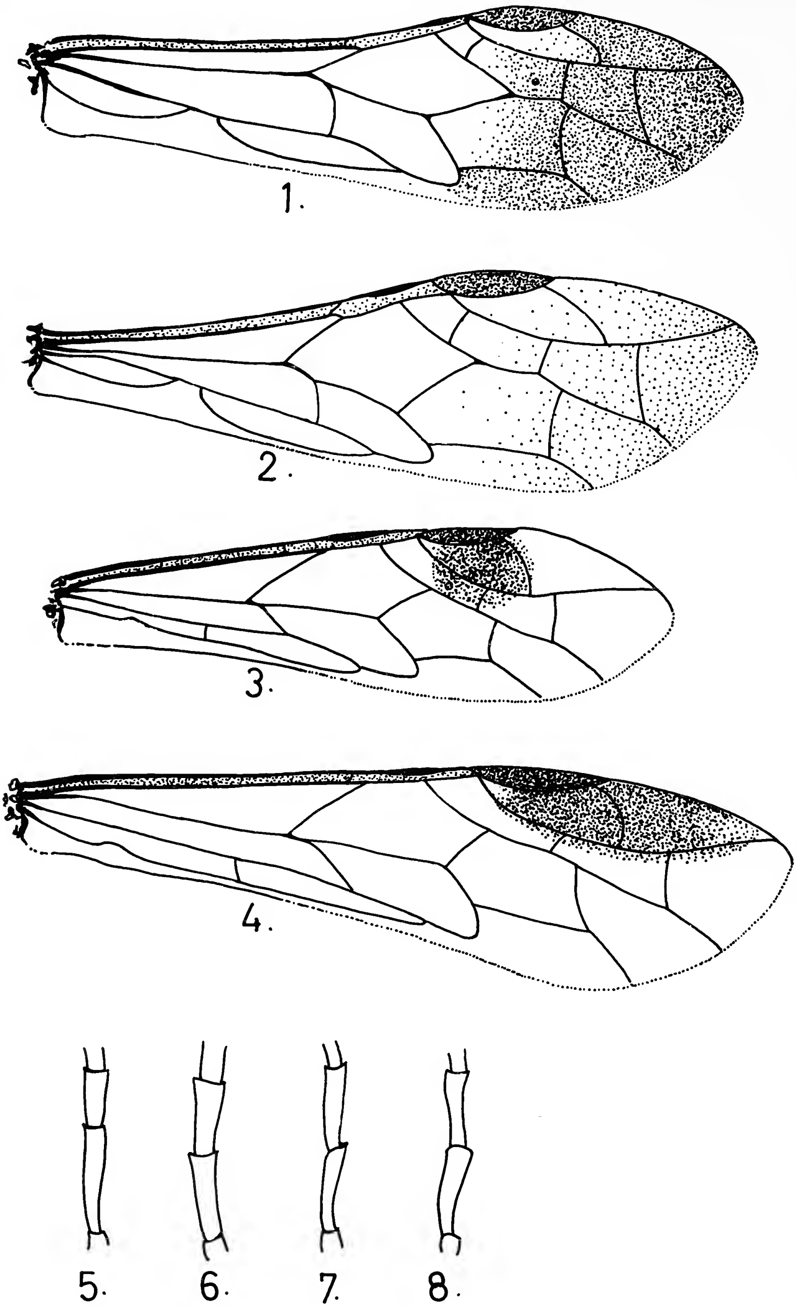
Material examined. Holotype ♂, 20.6.1983, collected from Mandal area (U.P.), India, 7,200 feet.

Etymology. The name is from the city near the type locality.

Macrophya concolor, new species

Description. Female: Length, 10.8 mm. Body black, yellowish brown areas as follows: labrum except irregular black spot in the middle of its proximal half and palpi. Yellowish white as follows: distal ⅔ of clypeus, posterodorsal pronotal angles, lateral spots on abdominal segments 2–8, lateral stripe on metacoxae, all trochanters, proximal and distal ends of four front femora, a longitudinal stripe along anterior border of profemur, four front tibiae anteriorly, metatibia with irregular spot on posterior side and proximal tips of metafemur. Forewing infuscated towards tip (Fig. 1), infuscation extending up to base of stigma, hindwing subinfumated toward tip.

Clypeus semicircularly incised (⅖ depth of its medial length), labrum convex in middle and deflexed along lateral sides having narrowly rounded anterior margin. Malar space wanting, inner margin of eyes emarginate and converging downwards, lower interocular distance ¾ of eye length; ratio of distances from posterior ocellus to eye, between posterior ocelli, and from posterior ocellus to hind margin of head 1.0:0.35:0.5. Antenna equal to 1.7× head width and incrassate in middle, segment 1 longer than broad, 2 as long as broad, 3 and 4 in the ratio 7:4 (Fig. 5), 4–9 gradually decreasing in length. Frontal area raised to level of eyes, inter- and circumocellar furrows indistinct, postocellar furrows faint, supra-antennal tubercles low, head car-



Figs. 1–8. 1. Forewing of *Macrophya concolor.* 2. Forewing of *Macrophya gopeshwari.* 3. Forewing of *Athlophorus bandatus.* 4. Forewing of *Athlophorus vespiformis.* 5. Third and fourth

inate and slightly converging behind eyes. Postocellar area broader than long in the ratio of 4:3.

Head with dense punctures all over, pronotum and mesonotum densely punctured, posterior slope of scutellum with deep and large punctures, area between punctures shining. Postscutellum with very minute punctures, mesopleuron with deep and dense punctures, sternum with punctures similar to notum, metapleuron and metasternum punctured similarly to mesosternum. Abdomen almost impunctate except lateral sides of first segment which are deeply and densely punctured. Except abdomen, body covered with silvery pubescence. Female lancet as in Figure 9.

Male: Length 9.2 mm; differs from female in having mesosternum with a triangular yellowish white spot, metacoxae anteriorly with white longitudinal irregular spots, mesocoxae almost yellowish white, pro- and mesolegs yellowish white anteriorly, metacoxa without a yellowish white lateral stripe, pronotal angles similar to body color, sternites 2–6 with yellowish white lateral stripes. Male genitalia (Figs. 11, 15).

Material examined. Holotype ♀, 15.6.1983, collected from Mandal area (U.P.), India, 7,200 feet. Paratypes: 1♀, 7♂♂ with same data as holotype.

Etymology. This species is named after its almost uniform body colour.

Remarks. These species do not key past couplet 9 in Malaise's key (1945). The following new section can be inserted to key out these species:

9. Scutellum with an acute, mostly edge-like transversal carina along the hind margin, mostly elevated into an acute point in the middle. The anterior margin of scutellum shallowly emarginate or subtruncate. Face between the eyes distinctly depressed below a level touching both eyes, and ocelli barely reaching that same level. The apical half of both wings strongly infumated. Head and thorax strongly and densely punctured, opaque. Sculpture of face almost wanting, and remnants of the antennal furrows remaining as punctiform and deep pits on each side of the indistinct frontal area. Postocellar area subconvex, narrowing anteriorly, the width behind compared to the length in the middle as 3:2; the lateral furrows very deep; the post- and interocellar furrows distinct, the former ones angulate. Head very strongly narrowing behind the eyes and there strongly carinate. Antennae as long as abdomen, distinctly incrassated and somewhat compressed in the middle, joints 3 and 4 as 4:3. Mesopleura bluntly raised below. Metaepimera without appendage. The hind metatarsi longer than all following joints combined. Black; the 5 basal segments of abdomen dark reddish. Yellowish white are: mouthparts, pronotal margins, base of tegulae, middle of scutellum, the anterior-side of the front legs, and on the hind legs: trochanters, a stripe on coxae, basal ⅔ of tibiae, basal half of femora in the ♀ and a stripe-like spot on the knees in both sexes. Length ♂ 8–9, ♀ 11–12 mm (20♂♂, 20♀♀). Burma (Shan States): Tonkin (Xieng Khouang: Ban Sai): 1,000–1,500 m .... *M. hastulata* Konow, 1898A

– Scutellum without transverse carina, clypeus shallowly to deeply incised, face not depressed viz., the frontal area hardly and ocelli not below a level touching both eyes 9a

9a. Clypeus black, mouthparts and labrum yellowish white, two yellowish spots on post-

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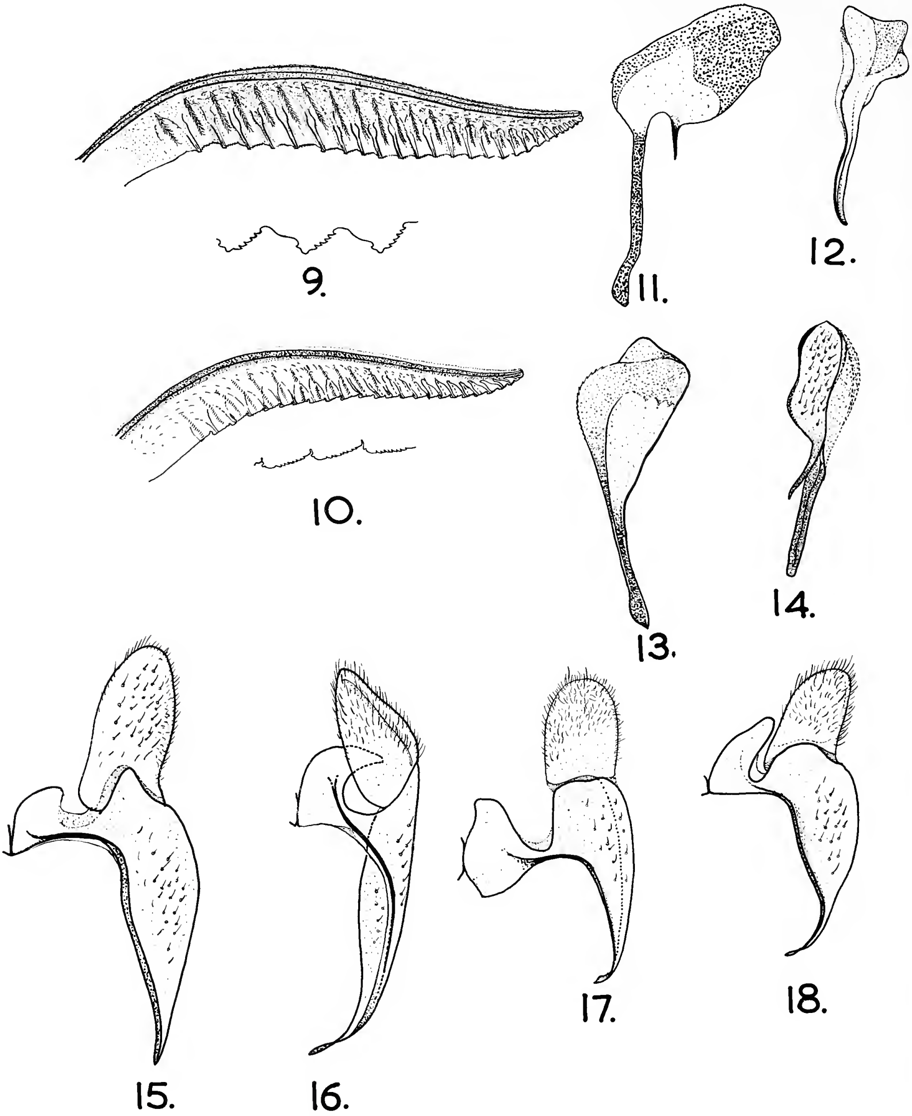
⟵

antennal segments of *M. concolor*. 6. Third and fourth antennal segments of *M. gopeshwari*. 7. Third and fourth antennal segments of *A. bandatus*. 8. Third and fourth antennal segments of *A. vespiformis*.



Figs. 9–18. 9. Female lancet of *Macrophya concolor.* 10. Female lancet of *Athlophorus vespiformis.* 11. Penis valve of *M. concolor.* 12. Penis valve of *A. vespiformis.* 13. Penis valve of *Macrophya gopeshwari.* 14. Penis valve of *Athlophorus bandatus.* 15. Harpe and parapenis of *M. concolor.* 16. Harpe and parapenis of *M. gopeshwari.* 17. Harpe and parapenis of *A. vespiformis.* 18. Harpe and parapenis of *A. bandatus.*

ocellar area. Yellowish-white V-shaped mark on posterior tip of mesonotal middle lobe. Abdomen brownish black with two yellowish spots on lateral side of first two segments. Forewing hyaline with apex weakly infumated. Head strongly converging behind eyes. Postoceller area as long as wide. Antennal segments 3 and 4 as 6:5. The hind basitarsus shorter than the following joints combined. Mandal (U.P.), India, 7,200 feet .... *Macrophya gopeshwari,* new species

– The hind basitarsus longer than the remaining tarsal joints combined 9b

9b. Distal ⅔ of clypeus black, basal ⅓ white, mouthparts and labrum yellowish brown, general colour black, yellowish white lateral spots on abdominal segments 2–8. Forewing strongly infuscated to base of stigma. Head slightly converging behind eyes. Postocellar area broader than long in the ratio of 4:3. Antennal segments 3 and 4 as 7:4. Forewing infuscated towards tip and infuscation extending up to base of stigma. Mandal (U.P.), India, 7,200 feet .... *Macrophya concolor,* new species

– If apex of wings is somewhat infumated then that infumation does not reach the base of stigma or is not conspicuous 10

ACKNOWLEDGMENT

The authors are deeply thankful to ICAR, New Delhi for the financial assistance to the project under which this work has been completed.

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Received June 15, 1984; accepted July 10, 1985.

J. New York Entomol. Soc. 94(1):70–77, 1986

RELATIVE ABUNDANCE OF ADULTS OF *CALLIRHOPALUS BIFASCIATUS* (ROELOFS) AND THREE *OTIORHYNCHUS* SPP. (COLEOPTERA: CURCULIONIDAE) ON CERTAIN CULTIVATED AND WILD PLANTS IN CONNECTICUT

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Abstract.—Adult weevils infesting cultivated and wild plants were sampled by dislodging them from foliage and by trapping them in pit-falls or under boards at six sites in Connecticut. The black vine weevil, *Otiorhynchus sulcatus* (F.), comprised 79–95% of the samples obtained by the three methods during June and July 1983. Less abundant species, which were concentrated on unsprayed plants, were: the strawberry root weevil, *O. ovatus* (L.); the rough strawberry root weevil, *O. rugosostriatus* (Goeze); and the twobanded Japanese weevil, *Callirhopalus bifasciatus* (Roelofs). *Otiorhynchus sulcatus* was the most abundant weevil on foliage of 71% of hosts surveyed in June and on 86% in July. Collectively, the results indicate that adults of *O. sulcatus* cause most of the foliar notching attributed to weevils. Possible wild reservoirs for *O. sulcatus* are given, and 17 new hosts for the four weevils are listed. Removal of adult hosts from field borders may minimize the establishment of wild reservoirs.

Shipment of nursery plants has increased the range of several exotic, flightless weevils (e.g., Maier, 1978). Even though nursery inspectors diligently search shipments for pestiferous weevils, they have little chance of detecting them if infestations consist of only a few adults in plant debris or a few eggs and larvae buried in the soil. In the absence of effective insecticides, undetected weevils, e.g., *Otiorhynchus* spp., can easily reach reproductive age because their host plants furnish food in the form of roots for larvae and foliage for adults. Infestations can be started by one or a few adults because many species are parthenogenetic and highly fecund (Smith, 1932; Maier, 1981, 1983b; Nielsen and Dunlap, 1981).

Recent increases in transcontinental shipping and interception of infested plants have caused Connecticut nursery inspectors to be concerned about what new weevils might be established in the state and what species are injuring nursery plants. The presence of new weevils may be difficult to detect because their foliar damage and larval appearance are likely to resemble those of the widespread black vine weevil, *Otiorhynchus sulcatus* (F.). Typically, after nurserymen or homeowners discover foliar notching, they make insecticide applications timed to control adults of *O. sulcatus.* No quantitative study exists to demonstrate if this weevil causes most of the injury or if spraying for it kills other weevils before they reproduce. This survey was undertaken to determine the identity and relative abundance of adult weevils that attack certain cultivated and nearby wild plants.

MATERIALS AND METHODS

Sampling for adults. Six Connecticut sites where weevils damaged plants in 1982 were sampled during June and/or July 1983. At each site, five pit-fall traps and five trap-boards (Maier, 1983a) were placed singly under different plants of each species sampled. The pit-fall traps, wax-coated cardboard cups measuring 11 cm across the circular top, were filled to about one-third of their depth with 200 ml of anhydrous isopropyl alcohol. Weevils that rested under boards during the day or that fell into pit-falls were collected twice weekly during two 2-week sampling periods: June 16 to 29 and July 16 to 29. In addition, on one night between June 16 and 23 and one between July 16 and 23, adults were dislodged from plants with a firm forehand blow and collected on a drop cloth. On each sampling occasion, 10 to 12 plant species per site were jarred for a total of 5 min/species between 2000 and 2200 hr EST when adults feed. Whenever possible, weevils were observed to confirm that they actually ate the foliage of plants upon which they rested. The Orange site (Table 1) was not sampled during June.

Weevils were identified by comparing them to published descriptions (e.g., Warner and Negley, 1976) and to a reference collection of known nursery pests: the twobanded Japanese weevil, *Callirhopalus bifasciatus* (Roelofs); the woods weevil, *Nemocestes* sp.; the strawberry root weevil, *Otiorhynchus ovatus* (L.); the rough strawberry root weevil, *O. rugosostriatus* (Goeze); the black vine weevil, *O. sulcatus*; and the obscure root weevil, *Sciopithes obscurus* Horn. Only weevils observed to eat leaves of cultivated plants were included in the analyses. This criterion excluded numerous billbugs, *Sphenophorus* spp., captured in pit-falls and two unidentified weevils captured on wild plants. Voucher specimens of the four species analyzed are deposited in the insect collection at The Connecticut Agricultural Experiment Station, New Haven.

Sampling sites. In Guilford, perennial ornamental plants, ranging in age from 2 to 10 years, were growing near the foundation of a house situated in a rural area. Hedgerows of *Forsythia* sp. and *Rosa multiflora* Thunb. were located about 10 m away. Both pit-falls and trap-boards were deployed under *Forsythia* sp., *Rhododendron* spp., *R. multiflora,* and *Taxus cuspidata* Sieb. and Zucc. No pesticides were applied between 1980 and 1983.

The site in New Haven was a large yard around a complex of buildings in a residential area. A more complete description is given by Maier (1978). Trapping devices were placed under *Cornus florida* L., *Ilex glabra* (L.) Gray, *Kalmia latifolia* L., *Pieris japonica* L., *Rhododendron* sp., and *T. cuspidata.* These plants, all at least 6 years old, were not sprayed with insecticides during the study. Only cultivated plants were sampled at New Haven and at Guilford.

Samples at Hamden were collected from a 4-year-old nursery and from wild plants within 50 m. Traps were distributed among *I. glabra, K. latifolia,* and *T. cuspidata* in the nursery and *R. multiflora* in the adjacent weedy field. During the 4 years of its existence, the nursery was not sprayed with pesticides.

The Orange site was a section of a commercial nursery. Many plants of *Rubus allegheniensis* Porter and other weedy species grew between the rows of ornamental plants. Sampling devices were deployed under *I. glabra, K. latifolia, Rhododendron* sp., and *T. cuspidata* in the rows and under *R. allegheniensis* between the rows. Two applications of acephate were made to the ornamental plants during 1983.

In Madison, sampling was conducted on nursery plants grown in containers, on shrubs grown for aesthetic purposes, and on wild plants situated around the container-grown ornamentals. Traps were placed along an embankment covered with *Cotoneaster dammeri* Schneid., under a hedgerow of *Chamaecyparis obtusa* (Sieb. and Zucc.), and under wild plants of *Berberis thunbergii* DC., *K. latifolia,* and *R. allegheniensis.* During summer 1983, acephate was applied at least twice to the container-grown stock and to *C. dammeri* and *C. obtusa.* The hedge of *C. obtusa* was not sprayed until June sampling was completed.

The location in Meriden was a nursery field surrounded by many species of wild plants growing along fencerows or in deciduous woods. Traps were placed under *P. japonica, Rhododendron* spp., and *T. cuspidata* in the commercial nursery and under wild *Celastrus scandens* L., *Cornus racemosa* Lam., and *R. multiflora* at the border of the forest. Ornamental plants grown for sale were sprayed three times with acephate during 1983. In addition, the area between rows of nursery plants was cultivated monthly during late spring and summer.

RESULTS

Among the weevils detected, *O. sulcatus* had the highest relative abundance in 32 (97%) of 33 collections obtained by the three sampling methods during June and July (Table 1). Adults of *O. sulcatus* represented 86% (range: 76–100%) and 80% (33–100%) of weevils captured on plants during June and July, respectively. This species comprised 92% (86–100%) and 79% (49–100%) of those in pit-falls and 95% (80–100%) and 94% (67–100%) of those under trap-boards during these respective months. Although the relative abundance of all species varied among sites and between months, *C. bifasciatus, O. ovatus,* and *O. rugosostriatus* usually represented only a small portion of each sample.

Otiorhynchus sulcatus occurred at all six sites, and *C. bifasciatus, O. ovatus,* and *O. rugosostriatus* at three (50%) each (Table 1). Overall, 95% of *C. bifasciatus* (N = 109), 100% of *O. ovatus* (N = 56) and *O. rugosostriatus* (N = 24), and 82% of *O. sulcatus* adults (N = 1,277) were collected on or under unsprayed plants. The three less widespread and less abundant weevils were associated mainly with unsprayed cultivated or wild plants at Guilford, New Haven, Hamden, and Madison although five (63%) of eight adults of *C. bifasciatus* from Orange were captured on or near sprayed plants.

All sampling techniques were successful for detecting *O. ovatus, O. rugosostriatus,* and *O. sulcatus* (Table 1). Trap-boards were least effective because they were not used as shelters by adults of *C. bifasciatus,* which remain on plants during the day. Of 1,416 weevils collected, trap-boards accounted for only 275 (19%), whereas dislodging and trapping with pit-falls yielded 692 (49%) and 449 (32%), respectively.

Otiorhynchus sulcatus was the most abundant of the four species in samples from 15 (71%) of 21 plant species that had weevils in June and from 18 (86%) of 21 that had them in July (Table 2). In June, *C. bifasciatus* dominated on four plants (19%), and *O. ovatus* on one (5%). In July, *O. ovatus* and *O. rugosostriatus* each represented the largest portion of adults dislodged from one (5%) plant species. During each sampling period, *O. sulcatus* and *O. rugosostriatus* were codominant on one cultivated species.

In the combined samples from June and July, *O. sulcatus* occurred on 22 (96%)

Table 1. Relative abundance (represented as % of total) of four weevil species captured by three methods at six Connecticut sites during June and/or July 1983.[a]

Location of sample	Month of sample	% of total represented by each species in samples obtained by:										
		Dislodging from plants				Trapping with pit-falls				Trapping with boards		
		C.b.	*O.o.*	*O.r.*	*O.s.*	*C.b.*	*O.o.*	*O.r.*	*O.s.*	*O.o.*	*O.r.*	*O.s.*
Guilford	June			21 (8)	79 (31)		11 (1)		89 (8)		20 (2)	80 (8)
	July			19 (5)	81 (22)			17 (1)	83 (5)			100 (8)
New Haven	June	14 (12)	1 (1)		85 (72)	12 (11)	1 (1)	1 (1)	86 (81)	4 (1)		96 (22)
	July	4 (6)	2 (3)	1 (2)	93 (138)	14 (11)	34 (27)	3 (2)	49 (39)	4 (3)	2 (2)	94 (77)
Hamden	June	24 (41)			76 (127)	3 (4)		1 (1)	96 (134)			100 (94)
	July	19 (12)			81 (52)	22 (4)			78 (14)			100 (24)
Orange	June											
	July	9 (5)			91 (49)	9 (3)			91 (28)			100 (17)
Madison	June		9 (2)		91 (21)		11 (2)		89 (17)			100 (2)
	July		67 (8)		33 (4)		28 (5)		72 (13)	33 (2)		67 (4)
Meriden	June				100 (26)				100 (8)			100 (2)
	July				100 (45)				100 (28)			100 (7)
Mean[b]	June	8	2	4	86	3	5	<1	92	1	4	95
	July	5	12	3	80	8	10	3	79	6	<1	94

[a] Abbreviations for weevil species are: *C.b.* = *Callirhopalus bifasciatus*; *O.o.* = *Otiorhynchus ovatus*; *O.r.* = *O. rugosostriatus*; and *O.s.* = *O. sulcatus*. Number of weevils is given in parentheses. Percentages are rounded to nearest whole number; values nearer to 0 than 1 are given as <1.

[b] Mean % represents the sum of each column divided by number of sites sampled (i.e., five in June and six in July).

Table 2. Relative abundance (represented as % of total) of weevils dislodged from cultivated and wild plants in Connecticut during June and/or July 1983.[a]

Identity of host plants		Sites where plants were sampled[b]
Family	Species	
Taxaceae	*Taxus cuspidata* Sieb. and Zucc.	G, N, H, O, Me
Cupressaceae	*Chamaecyparis obtusa* (Sieb. and Zucc.)	M
Ranunculaceae	*Paeonia* sp.	G
Berberidaceae	*Berberis thunbergii* DC.	H, M
Rosaceae	*Cotoneaster dammeri* Schneid.	M
	Rosa multiflora Thunb.	(G), H, Me
	Rosa sp.	G
	Rubus allegheniensis Porter	H, O, M
	R. occidentalis L.	H
Aquifoliaceae	*Ilex glabra* (L.) Gray	N, H, O
Celastraceae	*Celastrus scandens* L.	H, Me
Aceraceae	*Acer japonicum* Thunb.	M
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	H, M
Cornaceae	*Cornus florida* L.	N, O
	C. racemosa Lam.	H, Me
Ericaceae	*Kalmia latifolia* L.	N, H, O, (M)
	Pieris japonica (Thunb.) D. Don	N, (Me)
	Rhododendron spp.	G, N, O, (Me)
	R. impeditum Bald. f. and W. W. Sm.	N
Polemoniaceae	*Phlox* sp.	G
Labiatae	*Monarda* sp.	N
Solanaceae	*Solanum dulcamara* L.	H
Caprifoliaceae	*Viburnum* sp.	O

[a] Abbreviations for weevil species are: *C.b.* = *Callirhopalus bifasciatus*; *O.o.* = *Otiorhynchus ovatus*; *O.r.* = *O. rugosostriatus*; and *O.s.* = *O. sulcatus*. Number collected on each plant species is given in parentheses; percentages are rounded to nearest whole number.

[b] Sites are abbreviated as follows: G = Guilford, N = New Haven, H = Hamden, O = Orange, M = Madison and Me = Meriden. An underlined abbreviation indicates that a plant grew in the wild at that site. An abbreviation enclosed in parentheses denotes that the plant was sampled at that site but that no weevils were collected. Orange was not sampled in June.

of 23 plant species, *C. bifasciatus* on eight (35%), and both *O. ovatus* and *O. rugosostriatus* on three (9%) each (Table 2). *Otiorhynchus sulcatus* was the lone species obtained from 10 (43%) plant species, and *C. bifasciatus* was the only weevil from one (4%).

When weevil abundance was standardized by dividing total captures per plant species listed in Table 2 by the number of sites sampled, the mean number of *O. sulcatus* on *T. cuspidata* (58.4), *C. florida* (32.0), and *Parthenocissus quinquefolia* (L.) Planch. (29.5) was more than 2× that on other species. Similarly, the average number of *C. bifasciatus* on *R. multiflora* (12.0) and *C. florida* (10.0) was higher than that on other hosts.

At Orange, Madison, and Meriden, adults of one or more weevil species were associated with wild hosts that grew near sprayed ornamental plants (Tables 1 and

Table 2. Continued.

% of total comprised by each weevil in June				% of total comprised by each weevil in July			
C.b.	*O.o.*	*O.r.*	*O.s.*	*C.b.*	*O.o.*	*O.r.*	*O.s.*
			100 (122)				100 (141)
			100 (15)				100 (1)
		50 (5)	50 (5)			67 (4)	33 (2)
	25 (1)		75 (3)		100 (4)		
			100 (4)				100 (2)
67 (29)			33 (14)	48 (11)			52 (12)
			100 (2)				100 (4)
	100 (1)			18 (2)	36 (4)		46 (5)
100 (3)							100 (1)
			100 (7)				100 (15)
29 (2)			71 (5)	33 (1)			67 (2)
			100 (2)				
			100 (50)				100 (9)
48 (10)			52 (11)	12 (5)			88 (37)
100 (4)							100 (11)
22 (2)			78 (7)	13 (4)			87 (26)
						33 (2)	67 (4)
			100 (13)				100 (18)
			100 (3)				100 (4)
		27 (3)	73 (8)			50 (1)	50 (1)
	14 (1)		86 (6)		20 (3)		80 (12)
100 (3)							
							100 (3)

2). In the combined samples from Orange (Table 1), three (38%) of eight *C. bifasciatus* and six (6%) of 94 *O. sulcatus* were captured on or under *R. allegheniensis* plants growing in the nursery. At Madison, 13 (68%) of 19 *O. ovatus* and two (3%) of 61 *O. sulcatus* were associated with *R. allegheniensis* plants established at the border of sprayed areas. Another five (26%) *O. ovatus* were taken near *B. thunbergii.* At Meriden, 18 (16%) of 116 *O. sulcatus* were associated with wild plants growing in brushy areas adjacent to sprayed fields. Sixteen of these were present in the combined samples from *C. racemosa* Lam. bushes located within 3–5 m of infested *T. cuspidata.* Captures of *O. sulcatus* on or under wild *C. racemosa* increased markedly from one in June to 15 in July, suggesting either that weevils had dispersed from the infested *T. cuspidata* to the nearby *C. racemosa,* or that adults had emerged near *C. racemosa* in July.

Feeding by each weevil species was confirmed for each possible host listed in Table 2 except for *Acer japonicum* Thunb. and *P. japonica.* New feeding hosts for adults are: *C. bifasciatus—R. allegheniensis, C. scandens, C. racemosa,* and *Solanum dulcamara* L.; *O. ovatus—B. thunbergii* and *Monarda* sp.; *O. rugosostriatus—Paeonia* sp. and *Phlox* sp.; *O. sulcatus—C. obtusa, Paeonia* sp., *B. thunbergii, C. dammeri, R. multiflora, P. quinquefolia, C. racemosa, Phlox* sp., and *Monarda* sp.

DISCUSSION

The four exotic weevils captured in Connecticut are widely recognized as plant pests in North America and in other regions of the world (e.g., Smith, 1932; Wilcox et al., 1934; Allen, 1957; Warner and Negley, 1976). In Connecticut, *O. sulcatus,* the most abundant species, is surely responsible for most of the leaf injury to sprayed and unsprayed ornamental plants. Its relatively high abundance on plants growing in yards and nurseries corroborates previous reports of it as a pest in Connecticut (Britton, 1914; Johnson, 1941). Infestations of *C. bifasciatus* and *O. ovatus* have also resulted in foliar or root damage in Connecticut (Britton, 1910, 1932). As shown in this survey, every one of the four weevils feeds upon foliage of unsprayed plants. The recovery of *C. bifasciatus* in Orange apparently represents the first record of this species in a commercial nursery in the United States. Insecticide applications timed for *O. sulcatus* may not be effective against *C. bifasciatus* because adults of the latter emerge one month earlier (Maier, 1981, 1983b).

Even though the four weevils are highly polyphagous (Smith, 1932; Warner and Negley, 1976; Marrone and Zepp, 1979), their reproductive potential varies markedly on different feeding hosts (Cram and Pearson, 1965; Maier, 1981, 1983b; Nielsen and Dunlap, 1981). The capability of adults to recognize and use superior over poor hosts may influence dispersion. However, the number of host plant records per species (Table 2) is probably correlated principally with abundance (i.e., an abundant weevil is more likely to be sampled than is a less abundant one), not with actual host range. Interestingly, *C. bifasciatus* attains higher relative abundance on *R. multiflora* and *C. florida* than it does on other hosts, indirectly supporting Maier's (1983b) contention that the first two are among the better hosts for nourishing the reproductive development of this weevil. Similarly, the high reproductive potential of *O. sulcatus* on *Taxus* spp. (Maier, 1981; Nielsen and Dunlap, 1981) may account partly for its high abundance on these plants.

Cram and Pearson (1965), Maier (1981), Nielsen and Dunlap (1981), and others have shown that adults of *O. sulcatus* can lay eggs in the laboratory when they feed exclusively on the foliage of certain wild plants. However, evidence for the existence of wild reservoirs is scant. Cram and Pearson (1965) have observed that adults feed on weeds in peat bogs and have suggested that weeds might facilitate population increases. Smith (1932) has listed larval and adult hosts of *O. sulcatus,* including plants that could grow in the wild, but did not indicate under what circumstances his observations were made. In this study, I have witnessed feeding on several wild plants; and at Hamden, adults have emerged from soil beneath caged wild *R. multiflora* (unpubl. data). At Meriden, *O. sulcatus* may have dispersed from *T. cuspidata* to *C. racemosa.* Should *C. racemosa* be used as a larval host, a second reservoir would be documented.

Chemical annihilation of populations of *O. sulcatus* in nursery fields at Hamden, Meriden, and elsewhere might not provide lasting control because adults could walk from nearby wild reservoirs to cultivated plants (Maier, 1978). Nielsen and Dunlap (1981) have similarly suggested dispersal from wild grape to cultivated plants, but they have not shown that weevils attack grape in the wild. Collectively, available evidence suggests that removal of possible wild hosts growing near field borders should lessen the chances of adults colonizing wild plants and reinfesting nursery fields.

ACKNOWLEDGMENTS

I am grateful to D. Wagner and L. Rogers for their technical assistance. A special thanks is due to the Connecticut nurserymen who cooperated during the study by permitting access to their fields. R. Doss kindly provided specimens of pest weevils from the Pacific Northwest. Finally, I thank J. Anderson and R. Weseloh (Conn. Agric. Exp. Stn., New Haven) for their critical appraisal of an earlier draft of this paper.

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Received March 11, 1985; accepted July 9, 1985.

J. New York Entomol. Soc. 94(1):78–82, 1986

TWO NEW SPECIES OF *STICTOCHILUS* BERGROTH FROM ARGENTINA (HEMIPTERA: PENTATOMIDAE)

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Abstract.—A diagnosis of *Stictochilus* Bergroth, descriptions of *S. barbatus,* new species, and *S. bituberculatus,* new species, a key to species, and drawings of their genitalia are provided.

Stictochilus Bergroth, 1918, has been monotypic until now. The two new species described here are similar to *S. tripunctatus* Bergroth, but they differ in several respects, particularly in the genitalia of both sexes. A diagnosis is given for the genus.

Stictochilus Bergroth, 1918

Stictochilus Bergroth, 1918:305; Rolston et al., 1980:122 (key).

Type species. Stictochilus tripunctatus Bergroth, 1918, by monotypy.

Diagnosis. Third abdominal sternite pinched into mesial tubercle, apposed apically by posterior margin of metasternum. Metasternum produced ventrad, arcuate in profile, carinate mesially at least anteriorly (thickened along metacoxal cavities and therefore appearing bicarinate posteriorly in *barbatus*). Mesosternum weakly carinate mesially; carina bulbous or compressed into plate anteriorly (plate semicircular in *tripunctatus*). Prosternal carina bifurcating at coxae, the two parts diverging and continuing to anterior prothoracic margin. Ostiolar ruga on each side reaching about ⅗ distance from mesial margin of ostiole to lateral margin of metapleuron; ruga sulcate, apical termination distinct. Femora unarmed. First rostral segment lying entirely between bucculae; apex of second segment between procoxae and of fourth segment between mesocoxae. Antennae 5-segmented; first segment clearly surpassing apex of head. Juga projecting well beyond tylus, contiguous apically. Humeri not produced. Two distinct sorts of dorsal punctation, normal sized punctures generally distributed, fine interstictual punctures basally on pronotum and scutellum. Inferior ridge of pygophore prominently developed; pair of tubercles present posterior to inferior ridge; both inferior ridge and tubercles fully exposed from caudal view.

Comments. Stictochilus is similar to *Marghita* Ruckes, 1964, recently redescribed by Grazia and Koehler (1983). The two known species of *Marghita* are generally larger (14.5–18.2 mm long) than the three known species of *Stictochilus* (9.7–14.7 mm long), and have the humeral angles moderately produced laterad. The metasternum in *Marghita* is produced farthest ventrad near the posterior margin and slopes dorsad to the anterior margin, while in *Stictochilus* the metasternum is more nearly arcuate in profile.

KEY TO SPECIES

1. Posterior margin of pygophore from ventral view broadly and shallowly concave, entire (Fig. 2); from caudal view, posterolateral angles of pygophore with tuft of long hairs without black tubercle (Fig. 5); middle third of posterior margin of each basal plate shallowly concave, mesial third diagonally linear (Fig. 8) .... *barbatus,* new species
– Posterior margin of pygophore from ventral view mesially emarginate (Figs. 1, 3); from caudal view, posterolateral angles of pygophore with black tubercle, without dense tuft of long hairs (Figs. 4, 6); posterior margin of each basal plate either evenly convex or nearly straight between rounded lateral and mesial angles 2
2. Posterior margin of pygophore from ventral view with pair of black tubercles visible in mesial emargination (Fig. 1); from caudal view, pair of tubercles at posterior pygophoral margin forming narrow, parallel-sided space; black tubercle at each posterolateral pygophoral angle entire (Fig. 4); posterior margin of each basal plate evenly convex (Fig. 7) .... *bituberculatus,* new species
– Pygophoral tubercles not visible in mesial emargination from ventral view (Fig. 3); from caudal view, pair of black tubercles between posterior margin and inferior ridge widely spaced; black tubercle at posterolateral pygophoral angles denticulate (Fig. 6); posterior margin of each basal plate very slightly concave above 9th paratergite (Fig. 9) .... *tripunctatus* Bergroth

Stictochilus barbatus, new species

Figs. 2, 5, 8

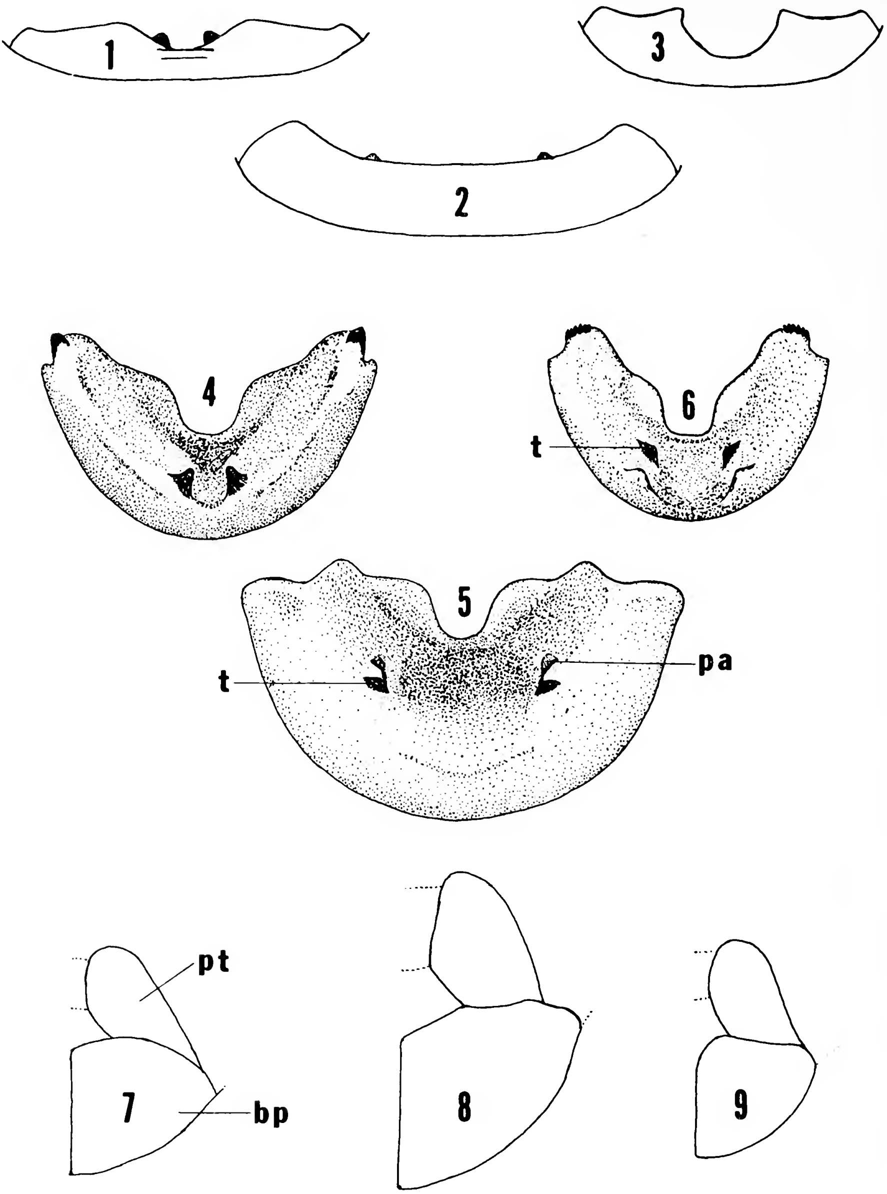
Description. Dark brown above, stramineous below; vague line on meson of pronotum continuing onto basal disc of scutellum and macule on hemelytral disc appearing slightly paler than adjacent areas; small mesial spot at base of scutellum yellowish; black mesial macule on each of segments 4–7 of abdominal venter subequal in size on female, much larger on segment 7 of male; small patch of black punctures located mesad of each spiracle.

Punctation on dorsum black. Punctures on head rather evenly distributed; on juga most in diagonal weak striae; few punctate striae on vertex or tylus. Pronotal punctation most dense cephalad of cicatrices, with fuscous suffusion from punctures in anterolateral angles; pronotal disc caudad of cicatrices and basal disc of scutellum weakly rugose with some punctures forming irregular transverse lines. Hemelytral punctation more uniform than on scutellum, with few lacunae. Legs and antennae stramineous with dark spots of various sizes. Rostrum stramineous, apex black.

Body broadest across abdomen; greatest width 7.3–8.2 mm; length excluding membranes 11.6–13.5 mm.

Lateral jugal margins only slightly concave before eyes, tapering sinuously to apex, nowhere parallel. Juga projecting well past tylus, contiguous apically but leaving small notch in apex of head. Width of head across eyes 2.7–3.0 mm, length 2.1–2.3 mm. Antennal segments 0.9–1.0, 0.9–1.0, 1.8–2.0, 2.1–2.4, 2.3–2.4 mm long. Rostrum reaching posterior margin of mesocoxae; segments 0.9–1.1, 1.2–1.6, 1.1–1.3, 0.8–0.9 mm long.

Anterior margin of pronotum behind interocular space of head raised into collar, this collar poorly defined in female; anterolateral margins straight, slightly reflexed. Humeral angles not produced, rounded. Width across humeri 6.5–7.3 mm, mesial length 2.6–2.8 mm.



Figs. 1–9. 1–3.—Posterior margin of pygophore, ventral view, vesture omitted. 1. *S. bituberculatus.* 2. *S. barbatus.* 3. *S. tripunctatus.* 4–6.—Pygophore, caudal view, vesture omitted. 4. *S. bituberculatus.* 5. *S. barbatus.* 6. *S. tripunctatus.* 7–9.—Basal plate and 9th paratergite. 7. *S. bituberculatus.* 8. *S. barbatus.* 9. *S. tripunctatus.* Symbols: basal plate (bp); pigmented area (pa); 9th paratergite (pt); tubercle (t).

Basal width of scutellum 4.0–4.4 mm, mesial length 4.7–5.4 mm; scutellar tongue 1.7–1.8 mm long, narrowly rounded at apex. Membrane of hemelytra fumose, veins fuscous.

Posterior margin of each basal plate shallowly concave along middle third, concavity in contact with 9th paratergite (Fig. 8); mesial margin reflexed. Each 9th paratergite angulate at junction with 2nd gonocoxa and 10th sternite. Tenth sternite subrectangular, longer than broad.

Posterolateral angles of pygophore without black tubercle but with dense tuft of long hairs. Posterior pygophoral margin shallowly concave from ventral view (Fig. 2). Short, black tubercle at posterior margin of pygophore about midway between each side and meson of pygophore, attended immediately entad by scarcely elevated black cusp (Fig. 5). Surface laterad of tubercle and between posterior margin and inferior ridge uniformly clothed with long hairs.

Holotype. ♂ labeled "Argentina, Salta, Abra Grande 4, 15, XII 967, Golbach Col." Deposited in Fundacion Miguel Lillo, Instituto de Zoologia.

Paratypes. ♂ and ♀, both labeled as holotype. ♂ deposited in American Museum of Natural History, ♀ in senior author's collection.

Stictochilus bituberculatus, new species

Figs. 1, 4, 7

Description. Brown to dark brown above; stramineous below but appearing darker due to dark punctures and suffusion from many punctures, especially on rather densely and finely punctate abdominal venter; 3 dark vittae present on abdominal venter, one mesial, one on each side just mesad of spiracles; lateral vittae poorly defined, continuing across thoracic pleura to eyes.

Punctures on dorsum fuscous to black. On head punctures irregularly spaced, most in diagonal striae on juga, in transverse striae on vertex and tylus, most fuscous, becoming crowded and black at ocelli. Most punctures caudad of cicatrices on pronotum and on scutellum in irregular transverse striae; narrow rugae separating striae on pronotum and basal disc of scutellum. Punctation of hemelytra denser and more uniform than on scutellum except scattering of small lacunae. Legs and antennae stramineous with darker spots of various sizes. Rostrum stramineous, black at apex.

Body broader across abdomen than across humeri; greatest width 6.4–6.9 mm; length excluding membranes 10.1–11.7 mm.

Lateral margins of juga sigmoid, nowhere parallel, notably concave before eyes, reflexed along anteocular concavity; juga projecting well beyond and contiguous before tylus but leaving small notch in apex of head. Surface of head slightly concave apically. Width of head across eyes 2.5 mm, length 1.7–2.0 mm. Antennal segments 0.6–0.8, 1.3–1.6, 1.4–1.7, 1.8–2.0 mm long. Rostrum reaching middle of mesocoxae; segments 0.7–0.9, 1.1–1.3, 0.8–0.9, 0.7–0.8 mm long.

Anterolateral margins of pronotum narrowly reflexed, nearly straight; anterior margin behind interocular space of head raised to form collar. Humeral angles not produced, rounded. Pronotal width across humeri 5.6–6.2 mm, mesial length 2.3–2.6 mm.

Scutellar width at base 3.5–3.9 mm, mesial length 4.5–5.0 mm; scutellar tongue

1.7–1.8 mm long; narrowly rounded at apex. Membrane of hemelytra fumose; veins fuscous.

Apical angles of abdominal segments somewhat rounded, scarcely produced. Spiracles large, oval, black.

Posterior margin of each basal plate convex (Fig. 7); mesial margin narrowly reflexed. Mesial margin of paratergite 9 uniformly convex. Sternite 10 subrectangular, longer than broad.

Pygophore with each posterolateral angle produced into short, entire, black tubercle (Fig. 1). Posterior margin from ventral view shallowly concave with pair of black tubercles visible in mesial emargination. These tubercles from caudal view at posterior margin, forming parallel-sided space (Fig. 4). Area between posterior pygophoral margin and inferior ridge concave, evenly clothed with long hairs.

Holotype. ♂ labeled "Argentina, Tucumán, San Ramón, XI-1947, Col. Garcia." Deposited in Fundacion Miguel Lillo, Instituto de Zoologia.

Paratype. ♀ labeled "Argentina, Salta, cerro San Bernardo 1.300 m. 3. VII 1969 Col. Weyrauch." Deposited in American Museum of Natural History.

ACKNOWLEDGMENT

We are grateful to Lic. Maria del V.A. de Toledo of the Fundacion Miguel Lillo, Instituto de Zoologia, San Miguel de Tucumán, República Argentina, for the opportunity to describe the new species deposited in collections under her supervision.

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Received January 16, 1985; accepted June 21, 1985.

J. New York Entomol. Soc. 94(1):83–97, 1986

BARYLAUS, NEW GENUS (COLEOPTERA: CARABIDAE) ENDEMIC TO THE WEST INDIES WITH OLD WORLD AFFINITIES

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Abstract.—The genus *Barylaus* is proposed for 2 endemic West Indian species of Carabidae; *Colpodes estriatus* Darlington (type species) from Puerto Rico, and *Colpodes puncticeps* Darlington from the Dominican Republic. The genus is described, and diagnoses and distributions of the species are presented. *Barylaus* is placed in the subtribe Caelostomina (tribe Pterostichini), based on synapomorphies shared with the genera *Mallopelmus* Alluaud, *Caelostomus* MacLeay, and *Hemitelestus* Alluaud. *Cyrtolaus* Bates is also transferred to the Caelostomina, making the subtribe pantropical. Based on an amphi-Atlantic vicariance hypothesis, the origin of the Caelostomina is estimated at 75–100 million years ago. A cladistic analysis is presented which supports the new subtribal limits. Recognition of the Caelostomina in the new sense results in the recognition of Pterostichini and Platynini as sister taxa.

In 1939, Philip Darlington wrote of a species of carabid beetle he had collected in the Dominican Republic:

> "This species is, in fact, completely isolated from all the species of Colpodes previously known to me, and I shall probably make it the type of a new genus in my final revision of the West Indian Carabidae" (p. 95).

Detailed examination of the mouthparts and internal reproductive structures of this and a related species from Puerto Rico indicates the need to propose a new genus in the tribe Pterostichini, subtribe Caelostomina Straneo (1942). In this paper, I describe the genus, and provide a key and diagnoses to the two known species. A cladistic analysis is presented which summarizes the derived character states of *Barylaus* shared with the Central American *Cyrtolaus* Bates, and exemplars of several Old World genera of the Caelostomina. Comparison of exemplar caelostomine taxa with the ground plans of the tribes Pterostichini and Platynini supports the recognition of these two taxa as sister taxa. Caelostomina in the new sense is expanded to include the endemic Neotropical genera *Barylaus* and *Cyrtolaus,* making the subtribe pantropical. A vicariance hypothesis provides an estimate of the age of the Caelostomina.

MATERIALS AND METHODS

Materials. Museum specimens were obtained with the assistance of the following curators, institutions, and individual collectors: George E. Ball and Danny Shpeley, University of Alberta (UASM); Ross T. Bell, University of Vermont (UV); Alfred F. Newton, Jr., Museum of Comparative Zoology, Harvard University (MCZ); Cornell University Insect Collection (CUIC); Julio Micheli, Ponce, Puerto Rico (JMi).

Methods. Whole specimens were examined using 8–100×. Male genitalia were dissected after clearing in cold 10% KOH and placed in glycerin for observation. Female reproductive tracts were cleared in cold KOH, stained in a Chlorazol Black suspension in methyl cellosolve, placed on a temporary glycerin slide with cover slip and examined using a dissecting microscope at low power, and a phase-contrast compound microscope at 100–200×.

The cladistic analysis was performed by hand using the Camin-Sokal algorithm (Sneath and Sokal, 1973) with the resultant procladogram modified to minimize steps. Transformation series polarities were determined by comparison of exemplar taxa with a wide range of out- and in-group taxa (Appendix I). A current classification of Carabidae (Erwin and Sims, 1984) permits estimation of likely out-groups, facilitating estimation of the primitive state of the characters (Watrous and Wheeler, 1981). For several exemplar taxa (Pterostichini, Platynini, *Cyrtolaus*) there are many possible generic or specific level taxa that could have been included. The tribes Pterostichini and Platynini are represented by what is considered the ground plan (Wagner, 1980) of each group. The ground plan is the minimal set of derived character states necessary to diagnose the group. The primitive character states for *Cyrtolaus* are taken from Whitehead and Ball (1975), or inferred from dissections of *Cyrtolaus subiridescens* Whitehead and Ball, and *C. ricardo* Whitehead and Ball.

Barylaus, new genus

Diagnosis. Compact shiny beetles with inflated convex elytra, cordate convex pronotum (Fig. 1), distinguishable from other Pterostichini by the following diagnostic characters: 1) elongate mouthparts; 2) frons and vertex with irregularly spaced pits; 3) pronotum without setae; 4) basal setigerous seta of elytron near base of 2nd interneur; 5) mesosternum with invaginated post-like apodeme (Fig. 8), evidenced externally by pit in mesosternum between fore-margins of mesocoxae; 6) elytra fused, metathoracic flight apparatus greatly reduced; 7) a series of large pits along lateral margins of elytra; 8) elytral plica developed internally, not visible externally as crossed elytral margin; 9) male copulatory organ inverted from typical pterostichine position, everted dextro-ventrally; 10) overall body length 4.0–7.0 mm.

Description. Body rotund, convex, head deflexed adding to round appearance. Body surface smooth, with reduced pronotal and elytral setation. Head elongate; frons with irregularly spaced pits; frontal furrows deep, clypeus somewhat inflated, separated from frons by impressed suture; labrum with 6 apical setae. Mandibles elongate (Figs. 2–5); right mandible bearing anterior, median, and posterior retinacular teeth (Fig. 3); both mandibles bearing 2 small dorsal pits. Maxilla with elongate lacinia, galea and palp (Fig. 6); lacinia with 2 peg-like setae accompanying thinner brush-like setae on internal margin; galea biarticulate, basal segment twice length of apical; palp with antepenultimate segment curved, thicker at middle, apical segment longer than penultimate. Labium (Fig. 7) with bisetose ligula; paraglossae membranous; palps 3-segmented, $3 > 2 > 1$ in length, apical segment inflated, palpiger nearly as long as 2nd segment. Mentum bisetose with well-developed pits. Antennae relatively short; scape with single apical seta, pedicel glabrous, antennomere 3 glabrous except for apical ring of setae, apical half of antennomere 4 and antennomeres 5–11 with fine dense setae.

Pronotum smooth, convex, cordate; lateral margins sinuate before nearly right or slightly acute, denticulate hind angles; median impression well developed, especially basally; latero-basal impressions smooth; basal bead absent; lateral setae absent; anterior transverse impression barely visible. Prosternal process broad, not margined, a broad median depression extending from between procoxae to near apical ⅓ of prosternum; sternum and episternum impunctate.

Elytra convex, fused, interneurs slightly impressed to not visible; scutellar interneur absent, basal elytral seta between 1st and 2nd interneur present; setae absent on elytral disc; a series of 5 or 9–10 pits situated along lateral margin of each elytron, the series of umbilicate lateral setigerous punctures interrupted by these foveae; lateral depression of elytron ending anteriorly at humerus; elytral plica developed internally (Fig. 15). Mesosternum somewhat pedunculate anteriorly; pit visible between anterior edges of mesocoxae which is due to large post-like apodeme (Fig. 8) which extends upward beneath the mesoscutellum. Metathorax short, metepisternum broader than long.

Legs relatively short. Pro- and mesocoxae with ventral condyle forming the ball of a ball and socket articulation. Femora moderately robust; tarsi not elongate, apical tarsomere with 2 pairs of ventral setae.

Abdomen heavily sclerotized; 1st and 2nd visible segments (segments II and III) fused laterally, segments III and IV fused medially; 3rd to 5th sutures with well-developed internal sulcus medially; apical sternite of females with 4 apical setae, males with 2 apical setae.

Male genitalia inverted from condition observed in noncaelostomine Pterostichini, the aedeagus everted to the right and then ventrally, lying in repose on the left side; parameres conchoid, glabrous, right paramere larger than left (Fig. 10). Female reproductive tract (only *B. estriatus* dissected) with biarticulate gonocoxae, the apical gonocoxite bearing 2 lateral and 1 dorsal setae (Fig. 13); basal gonocoxite bearing apical fringe of 4 to 7 setae. Spermathecal receptaculum with broad base joined to median oviduct near junction with bursa copulatrix, receptaculum base with fringe of ectodermal projections on hemocoelic surface; spermathecal gland duct entering near base of receptaculum.

Type species. Colpodes estriatus Darlington, described from El Yunque, Puerto Rico.

Generic name. Bary (heavy) + la-us (stone) alludes to the body shape of these beetles. The formation of the name emphasizes the affinities of *Cyrtolaus* Bates and *Barylaus.*

KEY TO THE ADULTS OF *Barylaus*

1. Elytral interneurs not visible, upper body smooth (Fig. 1); one seta over each eye; lateral margin of elytra with 5 large foveae; Puerto Rico .... *Barylaus estriatus*
1′. Elytral interneurs visible as linear impunctate impressions, elytral intervals broadly convex; no setae over eyes; lateral margins of elytra with 9–10 large foveae; Hispaniola .... *Barylaus puncticeps*

Barylaus estriatus (Darlington), **New Combination**

Colpodes estriatus Darlington, 1939, Mem. Soc. Cubana Hist. Nat. 13:96.

Diagnosis. In addition to key characters, distinguished from *B. puncticeps* by eyes of normal size, over 20 facets across diameter; aedeagus of male with median lobe

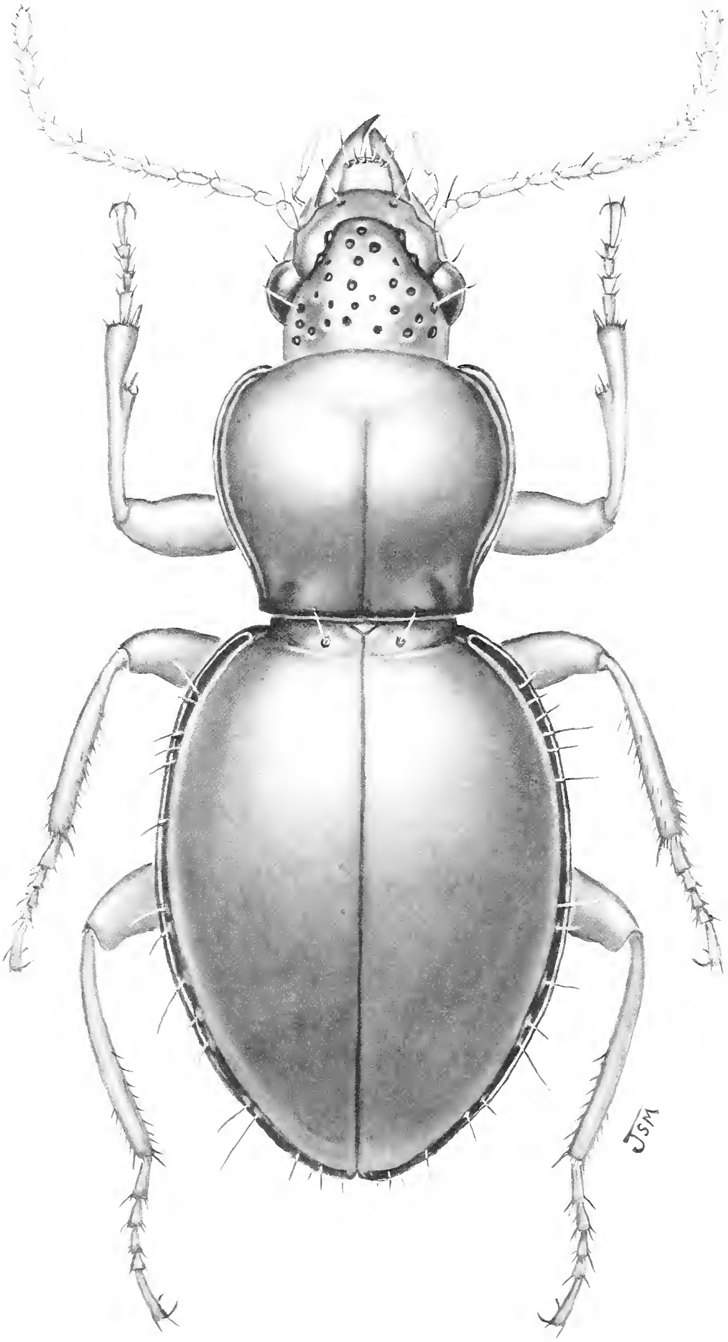
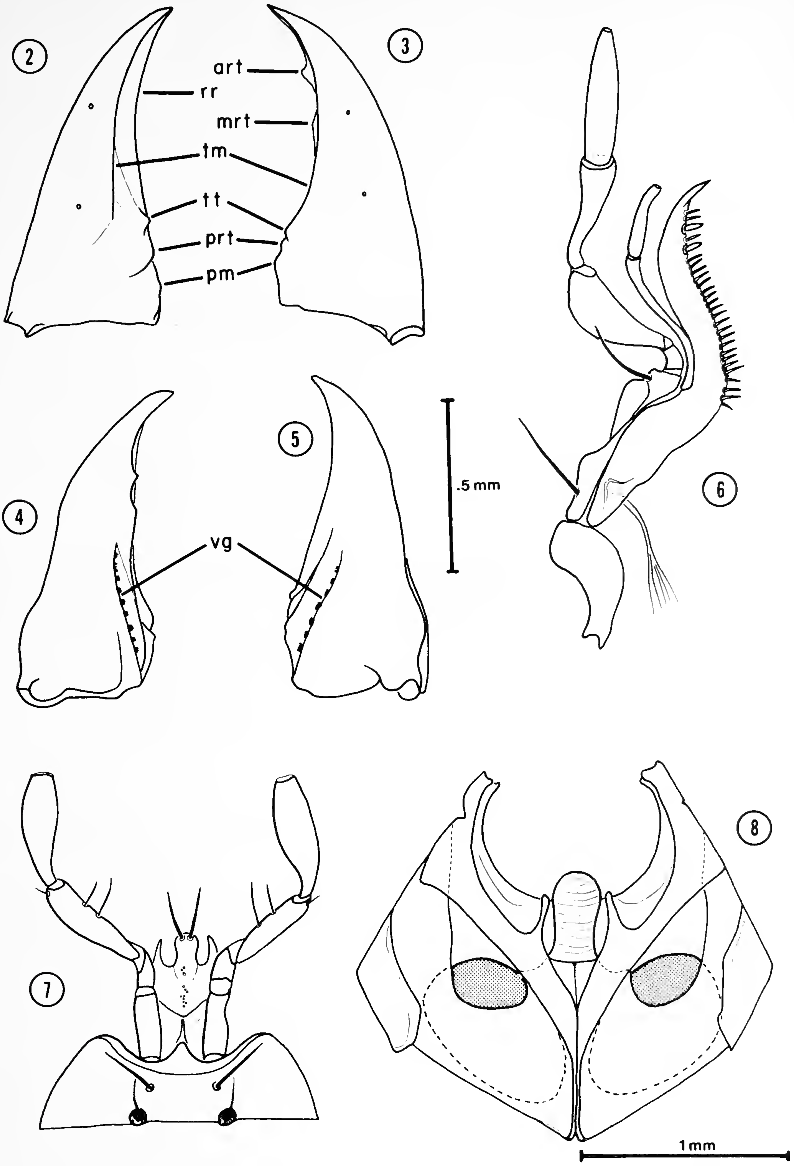


Fig. 1. Dorsal habitus of *Barylaus estriatus* (Darlington) female, El Yunque, Puerto Rico.



Figs. 2–8. 2–7. Mouthparts of *B. estriatus*. 2. Dorsal view of left mandible. 3. Dorsal view of right mandible. 4. Ventral view of right mandible. 5. Ventral view of left mandible. 6. Ventral view of right maxilla. 7. Ventral view of labium and mentum. (Scale bar is 0.5 mm; art = anterior retinacular tooth; mrt = median retinacular tooth; prt = posterior retinacular tooth; rr = retinacular ridge; tm = terebral margin; pm = premola; vg = ventral groove.) 8. Ental view from posterior of meta- and mesosternum, showing mesosternal post between mesocoxae. (Openings of coxal socket stippled; scale bar 1 mm.)

evenly curved (Fig. 9), small denticles near apex; internal sac of median lobe with basal band of sclerotized teeth and apical field of spicules surrounding gonopore.

Distribution records. PUERTO RICO: El Yunque, 3,000 ft elev., May 1938, Darlington (type series, 32 specimens); 3,000–3,300 ft elev., Feb 15–24, 1969, T. and B. Hlavac and L. Herman (3, MCZ); Jan 2, 1970, R. and J. Bell (3, UV); Caribbean Nat. For., Mte. Britton, 950 m elev., May 10, 1985 (3, CUIC), May 13, 1985 (10, CUIC), S. W. Nichols, E. R. Hoebeke, and J. K. Liebherr; Toro Negro For., Vereda el Bolo, 675 m elev., May 7, 1985, E. R. Hoebeke and J. K. Liebherr (3, CUIC); Guilarte For., April 20, 1975, J. Micheli, swept from foliage (1, JMi); Mte. Guilarte, base of summit trail, 925 m elev., May 5, 1985, S. W. Nichols, E. R. Hoebeke, and J. K. Liebherr (5, CUIC); Maricao For., 2,000–3,000 ft elev., Jun 2, 1938, Darlington (1, MCZ).

Biology and habits. Darlington (1939) reported *B. estriatus* running on rotten logs at night. All of the specimens collected in 1985 were associated with rotten logs or rotten palm fronds. Beetles were found on the underside of logs or fronds, often clinging upside down to the surface. Beetles were not found on the very wet to saturated soil surface.

The beetles exhibit a well-developed defensive posture when disturbed, in which they lie motionless with legs and antennae tucked against the body. This posture may be held for as long as 20 to 30 seconds.

Barylaus puncticeps (Darlington), **New Combination**

Colpodes puncticeps Darlington, 1939, Mem. Soc. Cubana Hist. Nat. 13:94.
Colpodes puncticeps compactus Darlington, 1939, *ibid.*:95.

Diagnosis. Key characters can be augmented by the following to diagnose *B. puncticeps*: eye reduced in size, approximately 9 facets across diameter; aedeagal median lobe of male with internal (ventral) margin swollen (Fig. 11), internal sac without sclerotized basal band of teeth or apical spicules.

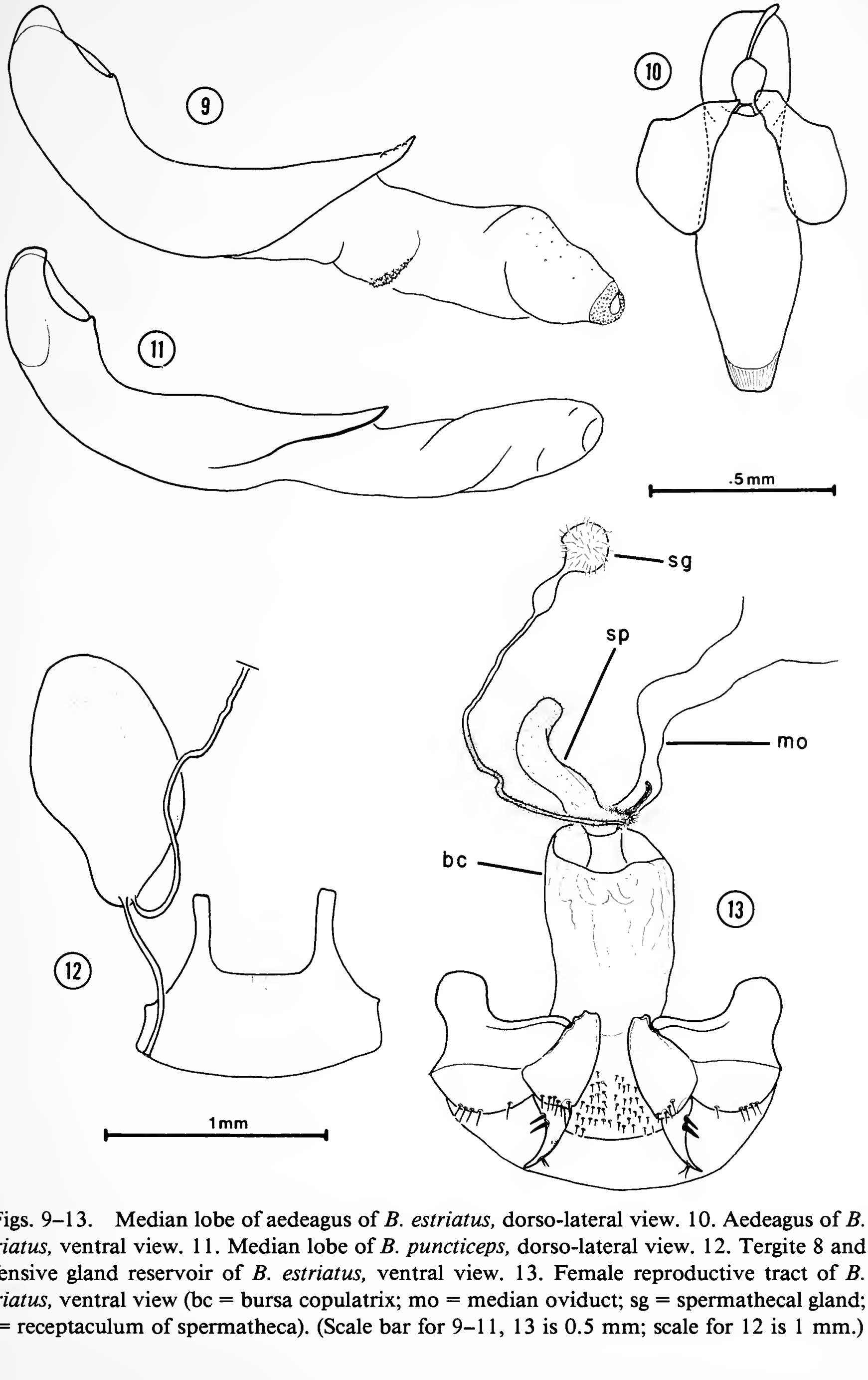
There are 6 known specimens of this species, of which I have seen 4: a male and female of each subspecies. Darlington (1939) lists differences in body part ratios which discriminate the two subspecies. Whether these differences represent geographic variation or inadequate sampling must await additional material.

Distribution records. B. p. puncticeps is known from DOMINICAN REPUBLIC: Loma Rucilla and mtns. N, 5,000–8,000 ft elev., June 1938, Darlington (type series, 3 specimens). *B. p. compactus* is known from D.R.: cloud forest vic. Valle Nuevo, ca. 6,000 ft elev., Aug 1938, Darlington (type series, 3 specimens).

PHYLOGENETIC AFFINITIES OF *Barylaus*

Straneo (1942) used the following characters to diagnose the pterostichine subtribe Caelostomina: 1) copulatory organ of male inverted; 2) umbilicate series on elytra interrupted toward the middle of their length; 3) setigerous pore at the base of the elytra positioned upon the third interval. Jeannel (1948) reports the Caelostomina as the only Old World Pterostichini (=subfamily Pterostichitae *sensu* Jeannel) possessing an inverted aedeagus.

Whitehead and Ball (1975) proposed the monogeneric subtribe Cyrtolaina to in-



Figs. 9–13. Median lobe of aedeagus of *B. estriatus*, dorso-lateral view. 10. Aedeagus of *B. estriatus*, ventral view. 11. Median lobe of *B. puncticeps*, dorso-lateral view. 12. Tergite 8 and defensive gland reservoir of *B. estriatus*, ventral view. 13. Female reproductive tract of *B. estriatus*, ventral view (bc = bursa copulatrix; mo = median oviduct; sg = spermathecal gland; sp = receptaculum of spermatheca). (Scale bar for 9–11, 13 is 0.5 mm; scale for 12 is 1 mm.)

Table 1. Character states for 12 characters and 7 taxa included in cladistic analysis (0 = primitive state; 1 = derived state).

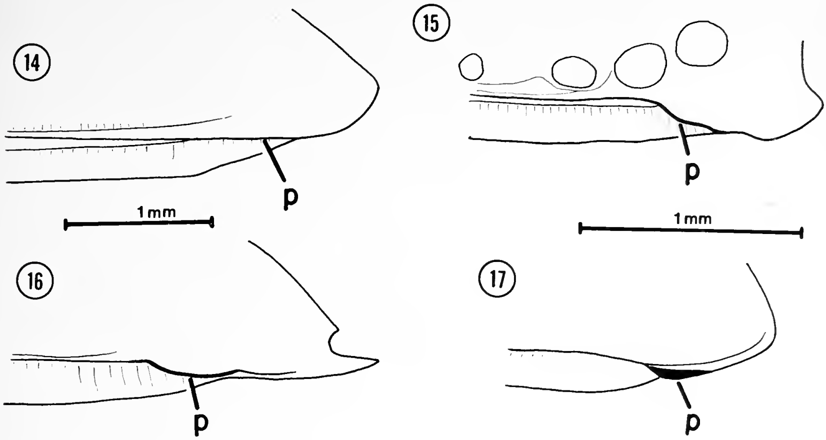
Taxon	Characters 1	2	3	4	5	6	7	8	9	10	11	12
Pterostichine ground plan	0	1	0	0	0	0	0	0	0	1	0	0
Cyrtolaus	0	1	1	0	0	0	0	1	1	0	0	1
Barylaus	0	0	1	1	0	1	0	1	1	0	1	0
Mallopelmus	0	1	1	1	0	1	0	1	1	0	0	0
Hemitelestus	0	1	1	1	1	1	1	1	0	1	1	0
Caelostomus	0	1	1	1	1	1	1	1	0	1	1	0
Platynine ground plan	1	0	0	0	0	0	0	0	0	0	0	1

clude *Cyrtolaus* Bates. This genus also exhibits the inverted aedeagus, but in general is more platynine-like, with the majority of the species possessing elytra without an externally visible plica. The Cyrtolaina were proposed as a subtribe that bridged the gap between the pterostichine and platynine lines, which in Whitehead and Ball's opinion necessitated inclusion of the Platynini within the Pterostichini.

To illustrate the phylogenetic relationships of *Barylaus* and these taxa, a cladistic analysis is presented which is based on the following taxa: 1) 3 taxa assigned by Straneo to the Caelostomina (*Mallopelmus* [*Trichillinus*] *linearis* Alluaud, *Hemitelestus hova* Alluaud, *Caelostomus picipes* MacLeay); 2) *Barylaus estriatus*; 3) *Cyrtolaus* spp.; 4) pterostichine ground plan; 5) platynine ground plan. The pterostichine and platynine ground plans are inferred from out-group comparison (Appendix I). Characters included are restricted to those possessed in derived state in 2 or more of the taxa. The characters and the rationale for assignment of character states are presented below. Character states of the taxa are summarized in Table 1.

Characters 1, 2. The elytral plica can be variously developed. In *Cicindela, Carabus, Nebria,* and *Blethisa* it is absent. Platynini and Harpalini also lack a plica, or any evidence of a lock mechanism on the internal surface of the elytra (Fig. 14). But, many taxa in the Carabinae possess an internal ridge that locks the abdomen and elytra (e.g., *Omophron, Loricera, Pasimachus, Patrobus, Diplous, Psydrus*). Thus at the level of the Pterostichini and Platynini the presence of an internally developed plica is considered primitive (Figs. 15, 16). Specialization is judged to have proceeded in 2 directions; 1) toward total absence of the plica internally or externally (states 1, 0; Fig. 14); 2) toward a fully developed externally visible plica as seen in most Pterostichini (states 0, 1; Fig. 17).

Character 3. The carabid lacinia generally bears fine brush-like setae on the inner margin of equal thickness throughout its length (state 0). In *Cyrtolaus, Barylaus, Mallopelmus, Hemitelestus,* and *Caelostomus,* there are 2 to 5 thicker peg-like setae on this margin near the lacinial tip in addition to the finer brush-like setae basally (Fig. 6; state 1). Straneo (1942) reports such setae from most Caelostomina, *Cosmodiscus* Sloane, and several other genera. Thicker setae are regularly spaced between fine setae along the lacinial margin in *Platynus veracrucensis* (Barr), a species with elongate mouthparts. But the thicker setae in *P. veracrucensis* are not as thick or



Figs. 14–17. Internal view of right elytral tip, showing internal development of plica (p). 14. *Platynus cychrinus* (Darl.). 15. *Barylaus estriatus* (Darl.) (circles above plica represent inner surface of elytal foveae). 16. *Cyrtolaus ricardo* Whd. and Ball. 17. *Caelostomus picipes* MacL. (Scale bar for 14, 16 on left, for 15, 17 on right.)

blunt relative to the fine setae as observed in *Barylaus.* Peg-like setae on the lacinia are also observed in *Ardistomis* (S. W. Nichols, pers. comm.), a genus characterized by elongate mouthparts. Such specialization of lacinial setae may be associated with elongation of mouthparts.

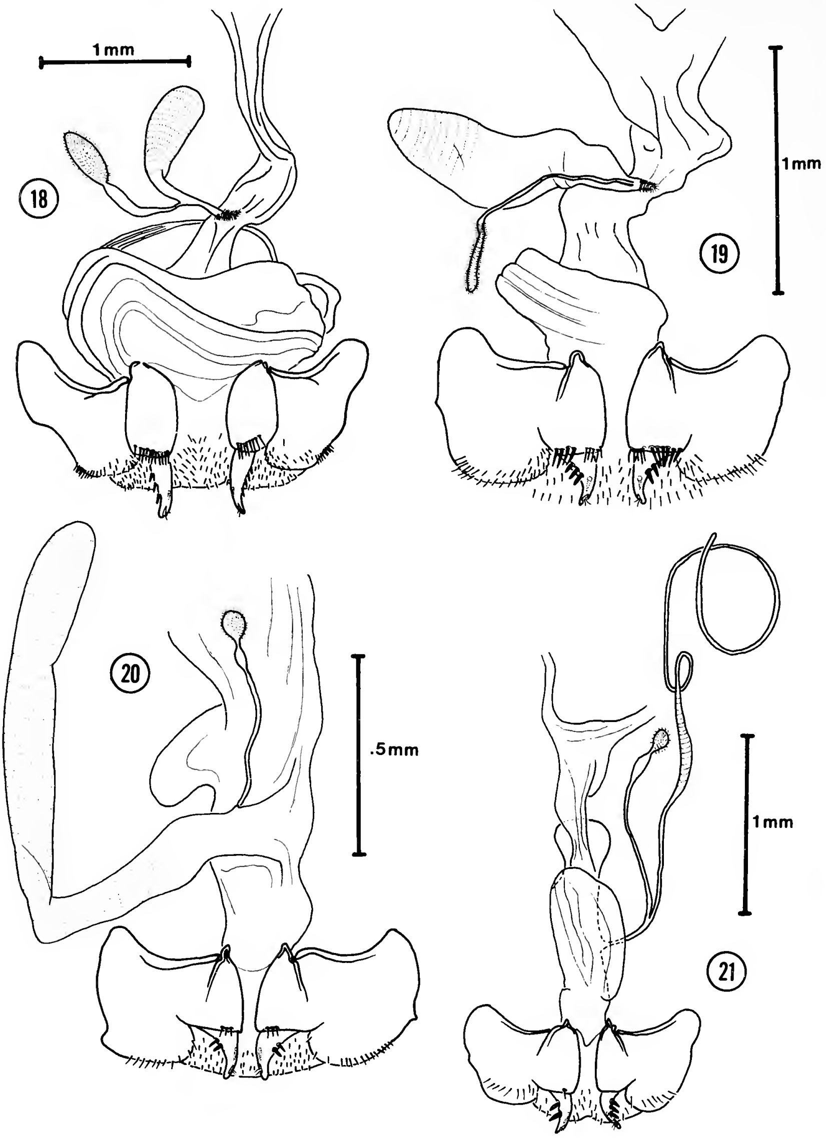
Characters 4, 5. The basal elytral seta is situated at the juncture of the interneurs 1 and 2 in most Carabidae (states 0, 0). With the fusion of the scutellar interneur to the base of the sutural interneur, this seta appears to be at the base of the 2nd interneur in *Barylaus* and *Mallopelmus* (states 1, 0). *Caelostomus* and *Hemitelestus* have this seta at the base of the 3rd interneur (states 1, 1).

Character 6. Dorsal elytral setae are observed throughout the Carabidae (state 0), whereas *Barylaus, Mallopelmus, Hemitelestus,* and *Caelostomus* possess no dorsal setae (state 1).

Character 7. Carabidae generally possess umbilicate elytral punctures on the apical half of the elytral margin that are not separated into distinct groups (state 0). *Caelostomus* and *Hemitelestus* have these setae positioned in 2 groups with a large intervening space without setae (state 1).

Character 8. Cyrtolaus, Barylaus, and the 3 Old World genera of Caelostomina have the aedeagus inverted (state 1) from the typical position seen in most Harpalinae. Reversal of the aedeagus is also observed in *Pristosia* Motschulsky (Lindroth, 1956) and *Calathus ovipennis* Putzeys (Ball and Negre, 1972), of the platynine subtribe Sphodrina. The derived nature of the styloid parameres in *Pristosia* and *C. ovipennis,* plus other characters, unite them with other Sphodrina, indicating that reversal of aedeagal position is a parallel derivation in these taxa.

Character 9. The setose-like patch of ectodermal filaments on the base of the spermatheca where it joins the median oviduct (state 1; Figs. 13, 18, 19) is known



Figs. 18–21. Female reproductive tracts, ventral view (scale bars with figures). 18. *Cyrtolaus ricardo* Whd. and Ball. 19. *Mallopelmus linearis* All. 20. *Caelostomus picipes* MacL. 21. *Hemitelestus hova* All.

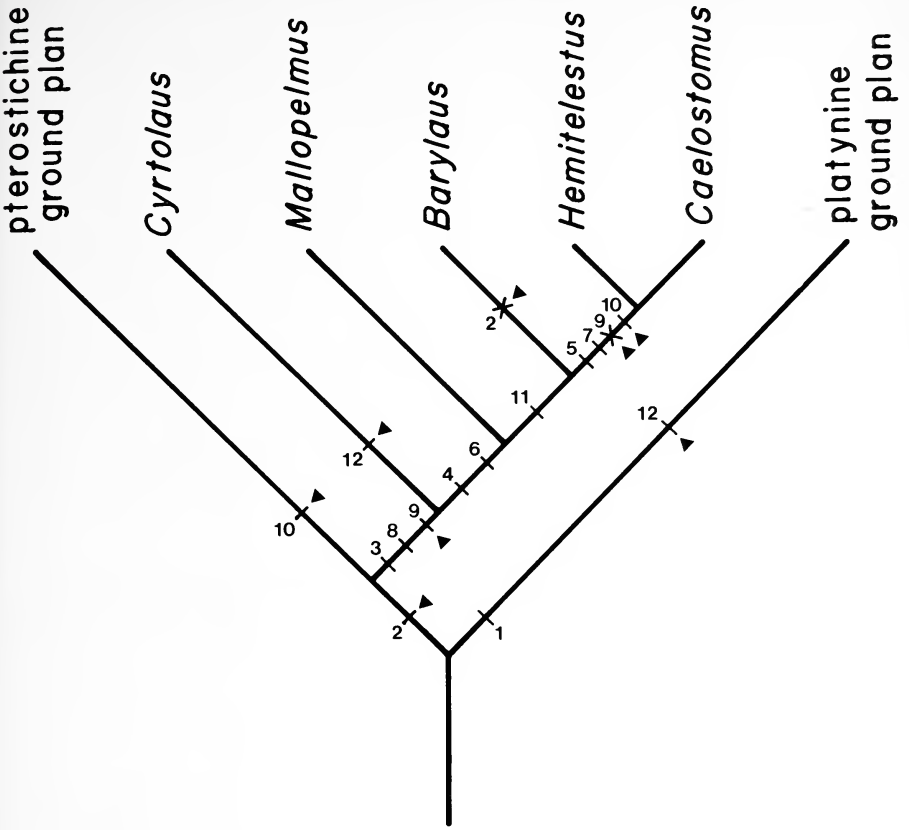


Fig. 22. Cladogram showing relationships of caelostomine genera to pterostichine and platynine ground plans (characters that change state more than once on cladogram have triangular flags; state gains shown by slashes, reversals to primitive state by x's).

only from *Cyrtolaus, Barylaus,* and *Mallopelmus. Cyclotrachelus sodalis* LeConte possesses a similar fringe with broader filaments, but this is assumed an independent derivation.

Character 10. The basal gonocoxite bears a fringe of setae in many Platynini and various carabid genera (e.g., *Carabus, Nebria, Blethisa, Thalassotrechus, Trechus, Patrobus, Amara,* and *Harpalus*). Glabrous or nearly glabrous basal gonocoxites are present in many Pterostichini and in *Caelostomus* and *Hemitelestus* (Figs. 20, 21). Reduction of the setal fringe is considered derived.

Character 11. The hemisternites of the 9th segment commonly bear many setae in more than one row (Figs. 18, 19). These setae are reduced to a single row in *Barylaus, Caelostomus,* and *Hemitelestus* (state 1; Figs. 13, 20, 21).

Character 12. The Platynini possess a well-developed dorsal lobe on the defensive gland reservoirs (state 1), a condition similar to that seen in the somewhat closely related Anthiini (Forsyth, 1972). Variously developed dorsal lobes are present in different tribes of the Harpalinae. *Cyrtolaus* also possesses such a lobe. The pterostichine defensive gland lacks the lobe, as in *Barylaus* (state 0; Fig. 12).

The most parsimonious cladogram places *Cyrtolaus, Mallopelmus, Barylaus, Hemitelestus,* and *Caelostomus* in one monophyletic group more closely related to the pterostichine ground plan than to the platynine ground plan (Fig. 22). There are 16 steps on the cladogram, with 4 characters changing state more than once. The development of an externally visible elytral plica is the only means of diagnosing Pterostichini. The loss of an internal elytral lock appears a derivation of the Platynini. In this analysis, *Cyrtolaus* is assumed to possess an elytral plica in fully developed condition, even though the more derived species within the genus have it in partially developed state (Fig. 16; Whitehead and Ball, 1975). Based on the most parsimonious cladogram, *Barylaus* has similarly lost a fully developed plica. The possession of an internal elytral plica in these taxa is considered a parallel secondary development. Other similarities of *Cyrtolaus* spp. and *Barylaus* include fused elytra, and very heavily sclerotized abdominal sclerites. With such developments, an internal elytral plica may suffice to strongly lock abdomen and elytra.

On the cladogram the derived character states of inverted aedeagus and lacinial peg-like setae unite *Cyrtolaus, Mallopelmus, Barylaus, Hemitelestus,* and *Caelostomus.* Based on these characters, plus the fringe on the base of spermatheca (character 9) and elytral setation (characters 4, 6), *Barylaus* is considered a member of the subtribe Caelostomina. A comprehensive study including all caelostomine genera is desirable, but the synapomorphies presented here strongly support such placement. *Cyrtolaus* is likewise best placed in the Caelostomina, although it possesses more primitive characters shared with the Platynini. The presence of a dorsal lobe on the defensive gland reservoirs in *Cyrtolaus* (character 12) does not support this placement. The occurrence of variously developed dorsal lobes in different lineages of the Harpalinae suggests parallel derivation of this character.

CONSEQUENCES OF CAELOSTOMINA IN THE NEW SENSE

The recognition of *Cyrtolaus* and *Barylaus* as New World representatives of the Caelostomina has several consequences. First, the Pterostichini and Platynini are best treated as sister taxa of tribal rank. The Pterostichini possess a well-developed externally visible elytral plica, which has apparently been reduced in several lineages. The Platynini is the more generalized taxon, which may also have spawned various lebiomorph lineages.

Secondly, if the statement of caelostomine relationships in Figure 22 is overlaid on the geographic distribution of the taxa included in the analysis (Fig. 23), an hypothesis of amphi-Atlantic vicariance can be proposed to account for the phylogenetic relationships. Both *Cyrtolaus* and *Barylaus* contain wingless upland species with very reduced metathoraces. This specialization occurs repeatedly in Carabidae, and based on the presence of wings in *Mallopelmus, Hemitelestus,* and *Caelostomus,* has occurred independently in *Cyrtolaus* and *Barylaus.* Nonetheless, amphi-Atlantic vicariance is a reasonable hypothesis. If it did occur, it would date the origin of the Caelostomina at late Cretaceous, 75–100 million years ago, when South America and Africa completed their separation (Smith et al., 1973; Anderson and Schmidt,

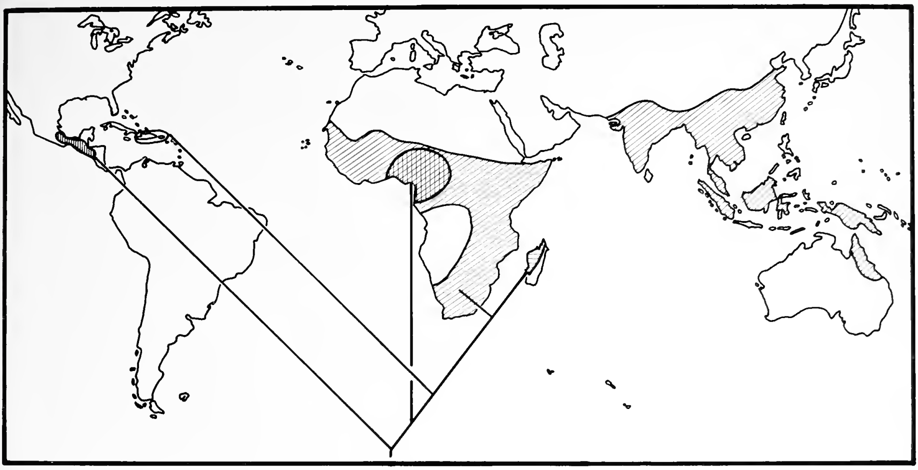


Fig. 23. Area-cladogram of 5 exemplar Caelostomine taxa: *Cyrtolaus* (dense vertical hatching); *Mallopelmus* (*Trichillinus*) (wide vertical hatching); *Barylaus* (open); *Hemitelestus* (horizontal hatching); *Caelostomus* (diagonal hatching).

1983). The great age of the Caelostomina is supported by the distribution of the 2 subgenera of *Mallopelmus*; sg. *Trichillinus* Straneo distributed in West Africa, and *Mallopelmus s. str.* restricted to Madagascar (Straneo, 1942). Madagascar reportedly rifted from the Kenya-Somalia coast at least 90 million years ago (Rabinowitz et al., 1983), a time estimate supporting an hypothesis of Cretaceous vicariance in this genus. The age of divergence for the Pterostichini and Platynini would predate the estimate for age of the Caelostomina.

Barylaus is more closely related to Old World taxa than it is to the Central American relict, *Cyrtolaus* (Figs. 22, 23). Such a result emphasizes the isolation of Puerto Rico and Hispaniola from Central America, especially when upland taxa are considered. It also emphasizes that geographic distribution should not color cladistic analysis.

Other insect groups in the West Indies exhibit African affinities. Brown (1978) summarizes butterfly distributions, concluding that several groups of long duration in the West Indies are as closely related to African as to Neotropical groups. Flint (1977) reports a small African influence in the West Indian faunas of Odonata and Trichoptera. The genus *Halocoryza* Alluaud (Carabidae: Scaritini) possesses an amphi-Atlantic distribution which includes the West Indies, but Whitehead (1966) attributes this distribution to past dispersal. *Caelostomus punctifrons* MacLeay, of West Africa, is introduced into Jamaica (Erwin and Sims, 1984). But, *Barylaus* and *Cyrtolaus* are poor candidates for long distance dispersal, as they both are comprised of upland flightless forest dwelling species of low population density. In specific, their biology, distribution, and phylogenetic relationships to Old World taxa strongly support an hypothesis of amphi-Atlantic vicariance. In general, they illustrate that Africa cannot be ignored when searching for nearest relatives of West Indian and Central American endemics.

ACKNOWLEDGMENTS

This paper is based partly on field material collected by Philip J. Darlington, Jr. This work would not have been possible without his pioneering work on the West Indian fauna, and so I respectfully dedicate this article to his memory.

Stephen W. Nichols has provided stimulating discussions of Caribbean biogeography, which led me to search Old World taxa as potential relatives of *Barylaus.* I also thank him for critical review of the manuscript, although any errors or oversights are my doing. James S. Miller rendered the habitus of *B. estriatus.* This project was supported by Hatch project NY(C) 139406.

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Received March 13, 1985; accepted June 6, 1985.

APPENDIX I

List of taxa used to polarize character transformation series and determine pterostichine and platynine ground plans.

Cicindela longilabris Say
Carabus nemoralis Mueller
Omophron dentatum LeConte
Nebria eschscholtzi Ménétriés
Blethisa multipunctata L.
Loricera foveata LeConte
Pasimachus elongatus LeConte
Bembidion planatum LeConte
Thalassotrechus barbarae Horn
Trechus chalybeus Dejean
Psydrus piceus LeConte
Patrobus longicornis Say
Diplous californicus Motschulsky
Synuchus impunctatus Say
Platynus cincticollis Say
Platynus decentis Say
Platynus veracrucensis Barr
Anchomenus picticornis Newman
Rhadine caudata LeConte
Agonum extensicolle Say
Myas coracinus Say
Pterostichus angustus Dejean
Pterostichus haldemani LeConte
Pterostichus lucublandus Say
Pterostichus menetriesi Motschulsky
Pterostichus stygicus Say
Abacidus permundus Say
Cyclotrachelus sodalis LeConte
Amara blanchardi Hayward
Harpalus erraticus Say
Anisodactylus discoideus Dejean

J. New York Entomol. Soc. 94(1):98–114, 1986

REVIEW OF THE TORTOISE BEETLE GENERA OF THE TRIBE CASSIDINI OCCURRING IN AMERICA NORTH OF MEXICO (COLEOPTERA: CHRYSOMELIDAE: CASSIDINAE)

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Abstract.—The tribe Cassidini is defined for the Western Hemisphere and the tribe Charidotini is united with it. A key is given for the fifteen genera known to occur in America north of Mexico. Two groups are recognized: the *Cassida* Group with six genera and the *Charidotis* Group with nine genera. *Metrionella* Spaeth, 1932, is recognized in North America for the first time, and a new genus *Opacinota* is proposed for *Coptocycla bisignata* Boheman, 1855. *Metriona* Weise, 1896, and *Nuzonia* Spaeth, 1913, are excluded from the North American fauna. *Metriona turba* Sanderson and King, 1951, is placed in synonymy under *Metrionella bilimeki* (Spaeth, 1932), *Metriona bicolor* (Fabricius) and *M. profligata* (Boheman) are transferred to *Charidotella,* and lectotypes are designated for *M. bilimeki* Spaeth and *Nuzonia ibaguensis* Spaeth, 1912.

The Cassidini is the largest and taxonomically most complex tribe of the chrysomelid subfamily Cassidinae. It is the only currently recognized tribe of Cassidinae with a worldwide distribution, containing 83 valid genera split nearly equally between the Eastern and Western Hemispheres (Seeno and Wilcox, 1982). More than 70% of the valid genus-group names are credited to Franz Spaeth and were published over a 53 year period between 1899 and 1952. Dr. Spaeth, before his death in 1946, is said to have completed a thorough taxonomic treatment of all the Cassidinae genera, but the only completed copy of this work was totally destroyed (Hincks, 1950, 1951). Working with a very incomplete second copy, Hincks (1952) published Spaeth's key to tribes and the last of Spaeth's generic and subgeneric descriptions. He also provided a listing of the world Cassidinae genera, which indicates the conclusions of Spaeth, and reviewed the type-species designations for all genus-group names.

Barber's (1916) synopsis of the North American Cassidinae, although containing much valuable information, is no longer satisfactory for identification purposes due to numerous taxonomic changes and a great quantity of new information. The key to genera given in Arnett (1968) for the United States, as well as those in the faunistic works by Wilcox (1954) and Balsbaugh and Hayes (1972), are no longer adequate considering recent contributions (Riley, 1982, 1985) and the new data presented here. The present work brings together new information in a format which includes diagnoses of the tribe and two generic groupings, a key to the North American genera, and appropriate discussions including distribution and host plant information.

Effort has been made in this work to insure the correct application of generic names to the North American fauna. Type-species for all North American genera have been examined as well as a wide cross section of species from the primarily neotropical genera. Additionally, representatives of most of the strictly neotropical genera have also been studied. The characters used in the key are combinations of those which define the genera in their entirety as well as those best distinguishing the North American representatives.

TARSAL CLAWS: TERMINOLOGY AND METHODS

The tarsal claws, great in their diversity of structure, are one of the most important diagnostic characters for the genera of the tribe Cassidini, and a clear understanding of the terms and techniques used in their study is necessary.

Tarsal claws which are said to be "appendiculate," or "toothed," possess a broad flange-like basal tooth while claws lacking this structure are termed "simple." Claws of a given claw-pair are "asymmetrical" when one claw is larger or differently shaped than the other, or more commonly, asymmetry is expressed in the development of the basal teeth.

Previous descriptions of asymmetrical claws of cassidine beetles have distinguished between individual claws of a given pair of claws by the terms "inner claw" and "outer claw," but these terms have remained undefined. The terms "anterior claw" and "posterior claw" are proposed as replacements for "outer claw" and "inner claw," respectively. The proposed terminology is much simpler and applies equally to fore, middle, and hind tarsal claws. Anterior and posterior claws are determined by visualizing, or orienting, a specimen into position with legs and tarsi projecting laterad, perpendicular to the longitudinal axis of the body, the claws widely divergent with the apices directed ventrad.

The claws of many species possess small, comb-like structures composed of a series of teeth arranged side by side (Figs. 14, 15). These tooth-combs are referred to as pectines. They vary considerably in size and development, and are clearly homologous with the larger combs of certain cassidine genera which are said to have "pectinate claws." The term "micropecten" was previously used (Riley, 1982, 1985) to describe the smaller, less conspicuous pectines.

When describing the presence or absence of pectines on a single claw or both claws of a given claw-pair, it is necessary to distinguish between the exterior and interior claw surfaces. Returning to the leg positioning mentioned above, those claw surfaces facing away from the beetle's longitudinal axis are the interiors while those facing towards the longitudinal axis are the exteriors. When pectines are said to be symmetrical, they are developed to a more or less equal extent on the anterior and posterior claws with respect to a particular surface. When pectines are asymmetrical, they differ significantly between the anterior and posterior claws with respect to a particular surface. The most commonly encountered asymmetry occurs when pectines are entirely absent from the exterior surface of the anterior claw while they are present and well developed on the other claw surfaces of the given claw-pair. Pectines are symmetrical for both surfaces in Figures 1–3; asymmetrical for exterior surfaces in Figures 5–7; and asymmetrical for both surfaces in Figure 8.

When pectines are small or poorly developed they may not be easily seen under high stereoscopic magnification. In these instances, the tarsus was removed, relaxed in hot 10% KOH, and examined while submersed in alcohol, glycerine or the KOH solution. This allowed rotation of the claws to various angles which exposed the pectines for viewing along the different claw margins. Mounting claws on microscope slides for examination with a compound microscope is the best technique and the one necessary for detailed examination. To prepare slide mounts, the tarsi or legs were removed from dried specimens, relaxed and lightly cleared for a few minutes in hot 10% KOH. The last tarsal segments were grasped with a fine tipped forceps and crushed just behind the base of the claws which articulate freely in the distal cavities of the segments. If care is exercised, the connecting tissue between the claws will remain intact keeping the claw-pair together in an easily managed condition. Claw-pairs were then transferred to drops of Hoyer's mounting medium on slides and oriented to the desired surfaces. Careful watch was maintained as cover slips were added to insure that the desired perspectives of the claws were retained while the cover slips settled. One fore, one middle, and one hind claw-pair were prepared simultaneously resulting in one slide mount per specimen. The final slides were examined with a compound microscope and the conditions of the claws recorded on code sheets by species and sex. Most slide preparations are maintained in the author's collection as permanent mounts for future reference. Illustrations (Figs. 1–8) were made from slide mounts with the aid of a one hundred unit ocular grid.

Tribe Cassidini

Hybosites Chapuis, 1875:380.
Cassidites Chapuis, 1875:383.
Chiridites Chapuis, 1875:405.
Aspidomorphites Chapuis, 1875:406 (in part).
Cassiditae Spaeth, 1914:129.
Coptocyclitae Spaeth and Reitter, 1926:7.
Charidotitae Spaeth, 1942:40.
Cassidini Hincks, 1952:330.
Charidotini Hincks, 1952:330. **New Synonymy.**

Diagnosis. Head horizontal or nearly so; clypeus horizontal; eyes on same level as clypeus or slightly above. Anterior margin of pronotum broadly rounded and concealing head from dorsal view, rarely emarginate (some South American species). Tarsal claws paired, divergent, otherwise highly variable, symmetrical for all tarsi or asymmetrical on middle and hind tarsi; pectines present or absent, when present symmetrical or asymmetrical for either or both surfaces, minute to moderate in size or large and conspicuous, i.e., the tooth-combs of pectinate claws.

Remarks. The above diagnosis defines the Cassidini including the Charidotini in the Western Hemisphere. The genera comprising the Charidotini do not deserve separate tribal status. The enlarged pectines, the primary diagnostic character on which the tribe Charidotini was based, is only the extreme of a range of character states. The configuration of pectines of the genera grouped in this tribe by Hincks (1952) is the same as that found in the genera of the Cassidini that belong to the *Charidotis* Group as defined in this paper. The above diagnosis, if it were applied to the Old World cassidine fauna, would also include the Aspidomorphini.

Somewhat unique to the Cassidini are the instances of asymmetrical claw-pairs. Such asymmetry occurs in the middle and sometimes the hind claws and is expressed to varying degrees depending on taxon and sex. The Dorynotini and Hemisphaerotini are the only other New World tribes which also have genera with asymmetrical claws. The asymmetry found in these tribes is fundamentally different from that in the Cassidini, occurring consistently in all tarsi of both sexes.

The Cassidini is clearly the most advanced tribe of the subfamily in that they possess a completely horizontal clypeus and concealed head. Although not all the genera have pectens, this is the only tribe (excluding the Old World Aspidomorphini) in which these structures are found. All genera of the Cassidini with enlarged pectens are here recognized in the generic grouping defined as the *Charidotis* Group; nevertheless, it is pecten asymmetry that defines the group, not pecten size (see group diagnosis). The aspidomorphine genera, which also have large pectens, are not closely related to the *Charidotis* Group. They appear to have been derived from the *Cassida* Group since both the Aspidomorphini and the genera of the *Cassida* Group have pectines symmetrical on both surfaces of the claws. Thus, it appears that the enlarged pectines have evolved independently at least twice, once in the Old World aspidomorphines and again in certain genera of the *Charidotis* Group of the New World Cassidini.

KEY TO THE NORTH AMERICAN CASSIDINI GENERA

1\. Anterior elytral margins crenulate 2
– Anterior elytral margins smooth 7
2\. Venter of pronotum with short groove on each side of head, each groove bordered externally by short carina 3
– Venter of pronotum without grooves 4
3\. Tarsal claws simple; elytra rugosely punctate or tuberculate .... *Parorectis*
– Tarsal claws simple but appearing appendiculate due to the distally projecting flanks of the claw segment (Fig. 13); elytra punctate-striate, smooth .... *Deloyala*
4\. Tarsal claws simple 5
– Tarsal claws appendiculate 6
5\. Apices of elytral epipleura with numerous ventrally projecting setae; elytra with common, post-scutellar protuberance .... *Coptocycla* (*Psalidonota*)
– Apices of elytral epipleura essentially glabrous; elytra evenly convex .... *Cassida* (s. str.) (in part)
6\. Antennae long and narrow, 8th segments distinctly longer than wide; elytra tuberculate and with common, post-scutellar protuberance .... *Plagiometriona* (*Parametriona*)
– Antennae short and thick, 8th segments as long as wide; elytra punctate-striate, non-tuberculate, evenly convex .... *Gratiana*
7\. Middle and hind tarsal claws distinctly pectinate (easily observed under normal magnification) .... *Microctenochira* (s. str.)
– Middle and hind tarsal claws not distinctly pectinate (pectines usually present to some degree but very small) 8
8\. All tarsal claws simple 9
– Claws of fore tarsi appendiculate; middle and hind claws variable, but with at least one claw toothed 12
9\. Male with anterior claw of middle tarsus much longer and of different shape than posterior claw; each elytron with three conspicuous maculae .... *Jonthonota*

– Male with claws of middle tarsus equal or subequal in size and shape; dorsum with vague maculae 10

10\. Head with fronto-clypeal sulcus absent and base of clypeus poorly defined .... *Cassida* (s. str.) (in part)

– Head with fronto-clypeal sulcus wide and deep, clearly delineating base of clypeus .. 11

11\. Elytral margins at apices projecting caudad in a shelf-like fashion, horizontal; epipleura at apices moderately wide, horizontal; elytral margins impunctate .... *Opacinota,* new genus

– Elytral margins at apices deflexed, not projecting in a shelf-like fashion; epipleura at apices narrower, deflexed; elytral margins distinctly punctate .... *Floridocassis*

12\. Male with middle tarsal claws symmetrical possessing equally developed basal teeth; species vittate .... *Agroiconota*

– Male with middle claws asymmetrical, at least one claw with simple or poorly developed tooth; species non-vittate 13

13\. Elytral margins at apices projecting caudad in a shelf-like fashion, horizontal; epipleura at apices moderately wide, horizontal; dorsum strongly alutaceous 14

– Elytral margins at apices deflexed, not projecting in a shelf-like fashion; epipleura at apices narrower, deflexed; dorsum usually shining, not strongly alutaceous 15

14\. Frontal groove crossing septum and continuing on clypeus as distinct median groove; lateral grooves of clypeus more evident; elytral margins impunctate .... *Strongylocassis*

– Frontal groove crossing septum but not continuing onto clypeus; lateral grooves of clypeus less evident; elytral margins deeply, confusedly punctate .... *Erepsocassis*

15\. Clypeus slightly swollen with distinct median groove; lateral grooves distinct and evenly impressed to base of clypeus (Fig. 12) .... *Metrionella*

– Clypeus flat or depressed in center, without distinct median groove; lateral grooves evident between posterior margin of eyes and bases of mandibles, not evenly impressed to base of clypeus .... *Charidotella*

Cassida Group

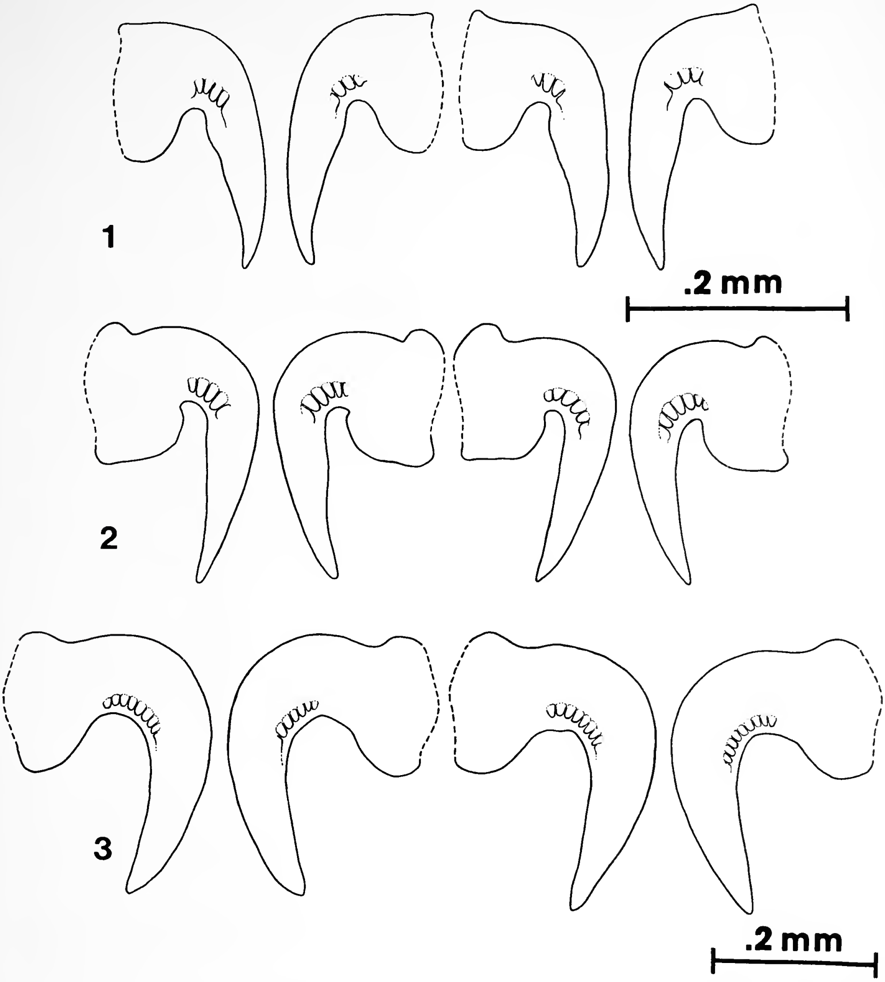
Diagnosis. Anterior elytral margins crenulate to some degree or rarely entirely smooth; all tarsal claws simple or appendiculate, always symmetrical in both sexes; pectens present or absent, when present always symmetrical on both surfaces.

Cassida Linnaeus

Cassida Linnaeus, 1758:362. (See Hincks, 1952, for the extensive synonymy of this primarily Old World genus.)

Three species belonging to the nominate subgenus are known to occur in eastern and central North America. These are the only true *Cassida* species occurring in the Western Hemisphere. *Cassida relicta* Spaeth is native to the nearctic region, *C. rubiginosa* Müller is a known introduction to North America, and *C. flaveola* Thunberg may have been introduced although this has not been documented. Known host plants for the North American species are Compositae and Caryophyllaceae.

The members of this genus have a wide range of variation in the development of the crenulations on the anterior elytral margins. In *C. flaveola* Thunberg the crenulations are greatly reduced or usually entirely absent. The pectens are present on the claws of some species while they are entirely lacking in other species.



Figs. 1–3. Left tarsal claws showing exterior and interior surfaces of anterior claw (on left) and interior and exterior surfaces of posterior claw (on right) of male, middle tarsi of genera belonging to the *Cassida* Group. 1. *Deloyala guttata*. 2. *Plagiometriona* (s. str.) *vigens*. 3. *Coptocycla* (*Psalidonota*) *texana*. Upper scale for Figures 1, 2; lower scale for Figure 3.

Coptocycla Chevrolat
Fig. 3

Coptocycla Chevrolat, 1837:396.
Thyreaspis Hope, 1840:158, 159.
Psalidonota Boheman, 1855:81 (subgenus).
Dyscineta Spaeth, 1936b:252, 260 (subgenus).
Podostraba Spaeth, 1936b:253, 259 (subgenus).
Coptocyclella Hincks, 1952:349 (subgenus).

Coptocycla is one of the three oldest generic names in the tribe Cassidini. As presently defined, it is a moderate sized neotropical genus divided into five subgenera. The single North American species is placed in the subgenus *Psalidonota.*

Originally proposed as a genus, *Psalidonota* was considered a subgenus by Spaeth (1936b) who recognized five species groups and 19 species. It is the best characterized of the five subgenera. Its species form a close assemblage sharing a distinctive habitus. All species are tumid, the elytra having a common post scutellar protuberance; the elytral discs are coarsely punctate, interspersed with impunctate pustulate areas; and the anterior margins of the elytra are deeply, distinctly crenulate. The pectens, which are usually absent or poorly developed in *Coptocycla* (s. str.), are well developed on the species of *Psalidonota.*

Coptocycla (*Psalidonota*) *texana* (Schaeffer) ranges from northeastern Mexico into south Texas (Cameron, Hidalgo, San Patricio and Aransas Counties) and as far north as Comal County, Texas. It feeds on the foliage of "anacua," *Ehretia anacua* (Teran and Berl.) I. M. Johnst., a small tree in the Boraginaceae.

Gratiana Spaeth

Gratiana Spaeth, 1913:142.

One species, *G. pallidula* (Boheman), is generally distributed throughout much of the United States. Known food plants belong to the Solanaceae. This genus is not a synonym of *Nuzonia* (see excluded genera).

Plagiometriona Spaeth

Fig. 2

Plagiometriona Spaeth, 1899:220.
Parametriona Spaeth, 1937:143 (subgenus).

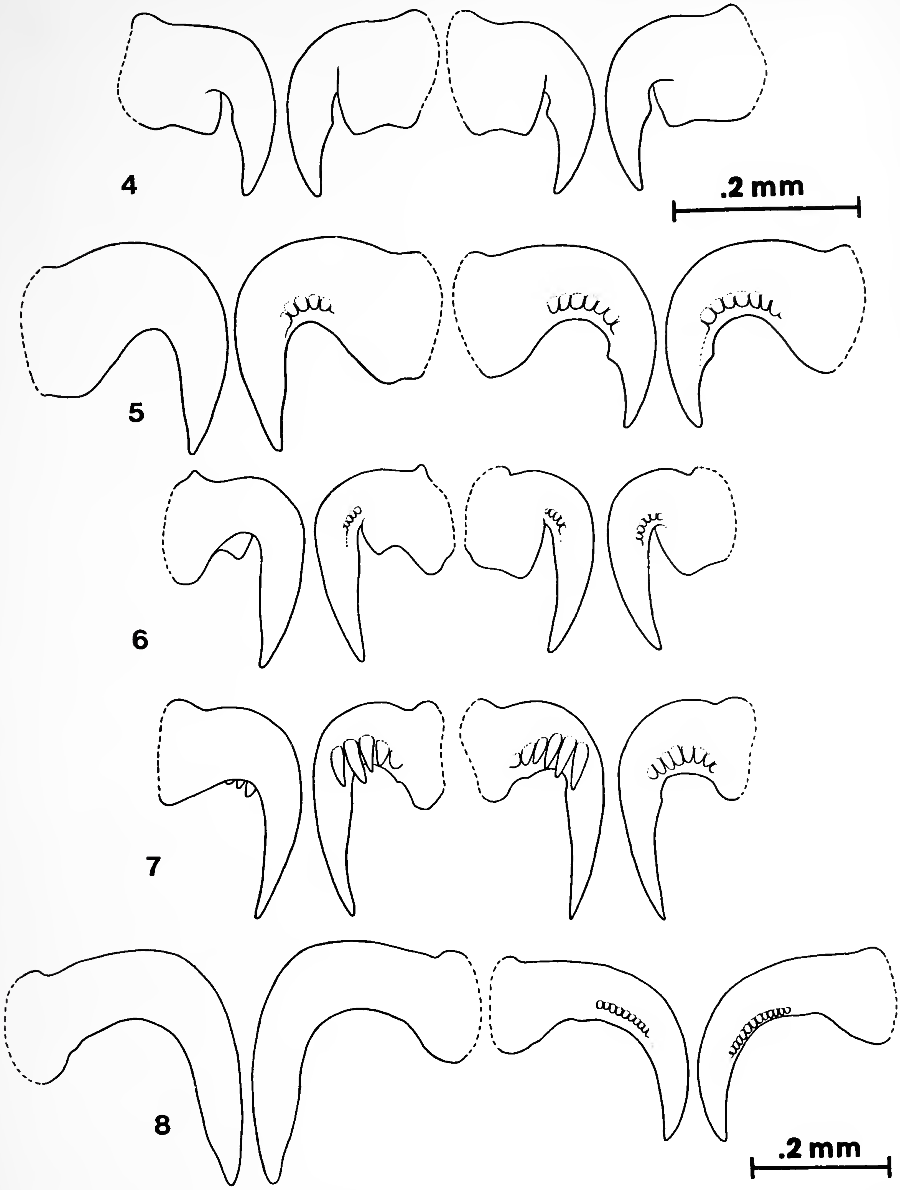
One species, *P.* (*Parametriona*) *clavata* (Fabricius) is generally distributed through the east, central and southern United States. Known food plants belong to the Solanaceae.

Plagiometriona is a large neotropical genus with about 80 species and is best represented in South America. Spaeth (1937) provided a key to the species groups and described the subgenus *Parametriona* in which he placed *clavata.*

Parorectis Spaeth

Parorectis Spaeth, 1901:346.
Orectis Spaeth, 1901:346 (nec Lederer, 1857).

Two of the three species comprising this genus occur in the southern United States: *P. callosa* (Boheman) is known from South Carolina, Florida, Texas (Barber, 1916), and Alabama (Balsbaugh and Hayes, 1972); *P. subleavis* (Barber), originally described from Texas, also occurs in Arizona (Portal, VIII-6; St. Rita Mts. VII-24), New Mexico (10.7 mi W Hope, VII-30), and Mexico (Sonora, 10 mi SE Agua Prieta, IX-15). Known food plants are Solanaceae.



Figs. 4–8. Left tarsal claws showing exterior and interior surfaces of anterior claw (on left) and interior and exterior surfaces of posterior claw (on right) of male, middle tarsi of genera belonging to the *Cassida* and *Charidotis* Groups. 4. *Agroiconota bivittata.* 5. *Floridocassis repudiata.* 6. *Metrionella bilimeki.* 7. *Microctenochira* (s. str.) *bonovoulori.* 8. *Jonthonota nigripes.* Upper scale for Figures 4–7; lower scale for Figure 8.

Deloyala Chevrolat
Figs. 1, 13

Deloyala Chevrolat, 1837:395.
Chirida Chapuis, 1875:405.

Four species are generally distributed throughout the United States and southern Canada. Food plants belong to the Convolvulaceae.

Agroiconota Spaeth
Fig. 4

Agroiconota Spaeth, 1913:142.

One species, *A. bivittata* (Say), occurs in the eastern, central and southern United States as well as in Mexico. This genus is included in the *Cassida* group on the basis of its symmetrical tarsal claws which entirely lack pectens (Fig. 4). All species seen thus far (14 in number) have smooth, non-crenulate, anterior elytral margins.

Charidotis Group

Diagnosis. Anterior elytral margins always smooth, never crenulate; tarsal claws simple or appendiculate, symmetrical or middle and sometimes hind tarsal claws asymmetrical to some degree in males and in females of some taxa; pectens present on middle and hind tarsal claws, always asymmetrical on exterior surfaces.

The neotropical genus *Charidotis* Boheman (1855) is the earliest described genus assignable to this group and is the basis for the name.

Jonthonota Spaeth
Fig. 8

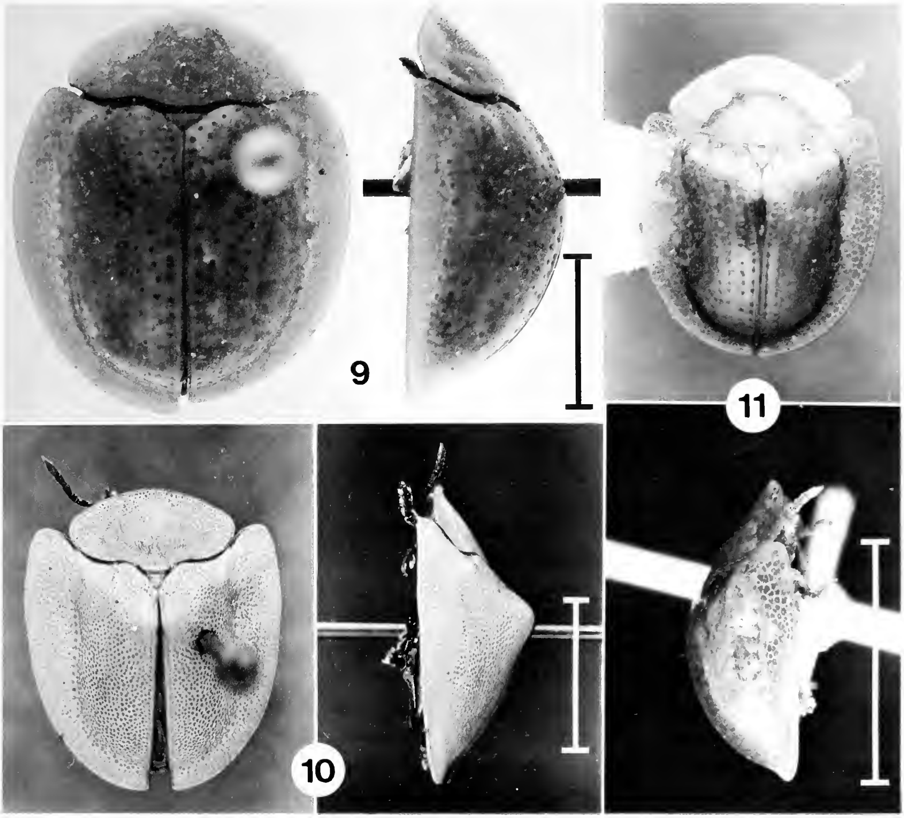
Jonthonota Spaeth, 1913:141.

Two species comprise this genus and both occur in the United States: *J. nigripes* (Olivier), transcontinental in distribution, and *J. mexicana* (Champion), found in Arizona, Texas (Davis Mts.), and Mexico. Host plants for *J. nigripes* are members of the Convolvulaceae.

Floridocassis Spaeth
Fig. 5

Floridocassis Spaeth *in* Hincks, 1952:348.

Floridocassis is monotypic, containing *F. repudiata* (Suffrian), which was originally described from Cuba and subsequently recorded from Florida (Barber, 1916) and Alabama (Balsbaugh and Hayes, 1972). Specimens have been examined from Alabama, Florida, Mississippi (Pearlington, III-19-1968), and South Carolina (Hilton Head Is., VII-2-1965). The distribution of this species is clearly coastal (Fig. 19) and is probably indicative of a close association with a plant species which is closely tied to coastal habitats. Balsbaugh and Hayes (1972) reported collecting *F. repudiata* from Convolvulaceae.



Figs. 9–11. 9. Lectotype, *Nuzonia ibaguensis*. 10. *Metriona elatior*. 11. Lectotype, *Metrionella bilimeki*. Scales = 4 mm.

Opacinota, new genus

Type-species, *Coptocycla bisignata* Boheman, 1855. Distribution (Fig. 17).

Continued study of the neotropical genera possessing simple claws has failed to reveal an existing genus suitable for *C. bisignata*. To accommodate this species, the new genus *Opacinota* (from Latin *opacus*—dim or obscure, and Latin *nota*—mark; gender feminine) is proposed. Illustrations and a description of the important taxonomic characters, as well as the taxonomic history of *C. bisignata* were given earlier (Riley, 1985), but a new genus was not proposed at that time.

Description. Head with frontal groove extending across septum and terminating in shallow notch on basal margin of clypeus. Fronto-clypeal sulcus wide and deep, nearly horizontal. Basal margin of clypeus raised well above, and projecting slightly over fronto-clypeal sulcus on either side of septum; lateral basal corners obtuse-angulate. Mesial surface of clypeus flat; lateral grooves poorly defined, evident near posterior edge of eyes. Elytra with anterior margins smooth; explanate margins impunctate, moderately to strongly deflexed anteriorly, becoming narrower and more

Table 1. Summary of character states for five monotypic genera of the tribe Cassidini, *Charidotis* Group.

Character[1]	*Erepsocassis*	*Floridocassis*	*Mexicaspis*[2]	*Opacinota*	*Strongylocassis*
Some tarsal claws toothed (all claws simple)	+	−	+	−	+
Elytral margins punctate (impunctate)	+	+	−	−	−
Elytral epipleura at apices moderately wide, horizontal (narrower, deflexed)	+	−	−	+	+
Pronotal corners angulate in male (rounded)	−	+	+	−	+
Clypeus with median groove (without groove)	−	−	−	−	+

[1] Positive character states presented first followed by the negative condition in parentheses.
[2] A Mexican genus.

horizontal posteriorly until apices where they project caudad in a shelf-like fashion. Epipleura at apices moderate in width, horizontal and glabrous; anterior inner edge entire, not modified to engage with metepisternum. All claws of both sexes simple; male with anterior claw of middle tarsi slightly larger than posterior claw; pectines absent (usually) or very poorly formed on internal surfaces of front tarsal claws, absent from external surfaces of anterior claws of middle and hind tarsi, present and well developed on other surfaces of middle and hind claws. Internal sac of aedeagus without sclerotized process.

This is the fifth genus of a group of monotypic genera whose species are strikingly similar in general appearance. The character states separating the five genera are summarized in Table 1. Host plants of *O. bisignata* are members of the Convolvulaceae.

Strongylocassis Hincks

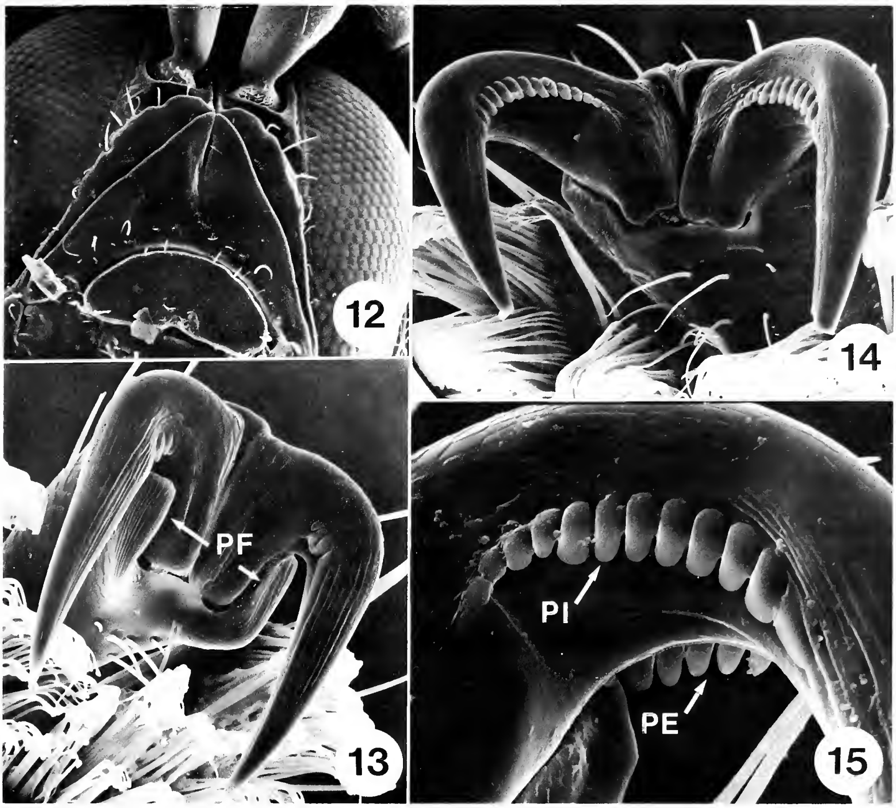
Stronglyaspis Spaeth, 1936a:216, 259 (nec Thomson, 1860).
Strongylocassis Hincks, 1950:511 (new name for *Strongylaspis* Spaeth, 1936).

Strongylocassis is monotypic containing *S. atripes* (LeConte) which is found throughout most of the central and eastern United States north to southeastern Canada. Known food plants are members of the Convolvulaceae. The taxonomy of this genus and species was reviewed earlier (Riley, 1985).

Erepsocassis Spaeth

Erepsocassis Spaeth, 1936a:260.

Erepsocassis is monotypic containing *E. rubella* (Boheman) which is known from several southeastern states (Fig. 6). Host plants have not been reported for this species. The taxonomy of this genus and species was reviewed earlier (Riley, 1982).



Figs. 12–15. 12. SEM of clypeus of *Metrionella bilimeki.* 13. Male, middle tarsal claws of *Deloyala guttata.* 14. Male, middle tarsal claws of *Charidotis* sp. 15. Posterior claw of male, middle tarsus of *Charidotis* sp. PF = projecting flanks, PI = pecten of interior claw surface, PE = pecten of exterior claw surface.

Metrionella Spaeth

Figs. 6, 11, 12

Metrionella Spaeth, 1932:263.

Metrionella bilimeki (Spaeth) is primarily a Mexican and Central American species which ranges north into southeastern Arizona and is the only species of *Metrionella* that occurs in America north of Mexico (Fig. 18).

Originally proposed as a subgenus of *Metriona* Weise, 1896, *Metrionella* was later listed as a full genus by Spaeth (*in* Hincks, 1952). It has not been previously reported from north of Mexico since *M. bilimeki* has been known by the name *Metriona turba* Sanderson and King, 1951. The holotype, allotype and two paratypes of *M. turba* [SEMC], and the syntypes of *M. bilimeki* [Spaeth Coll., Manchester Museum] have been examined and it is clear that the two names are synonyms, NEW SYNONYMY. Since Spaeth failed to indicate a holotype, a male (Fig. 11) labeled "Guatemala"

"Bilimeki m. Typus Spaeth det." "Typus" is here designated as lectotype and so labeled. The remaining 15 syntypes are designated as paralectotypes and appropriately labeled.

Food plants have not been reported for *M. bilimeki*; however, the writer has taken this species and the type-species of the genus, *Metrionella erratica* (Boheman), on unidentified Convolvulaceae in Mexico.

Charidotella Weise

Charidotella Weise, 1896:13.
Philaspis Spaeth, 1913:142 (subgenus).
Xenocassis Spaeth, 1936a:260 (subgenus).
Chaerocassis Spaeth *in* Hincks, 1952:350 (subgenus).

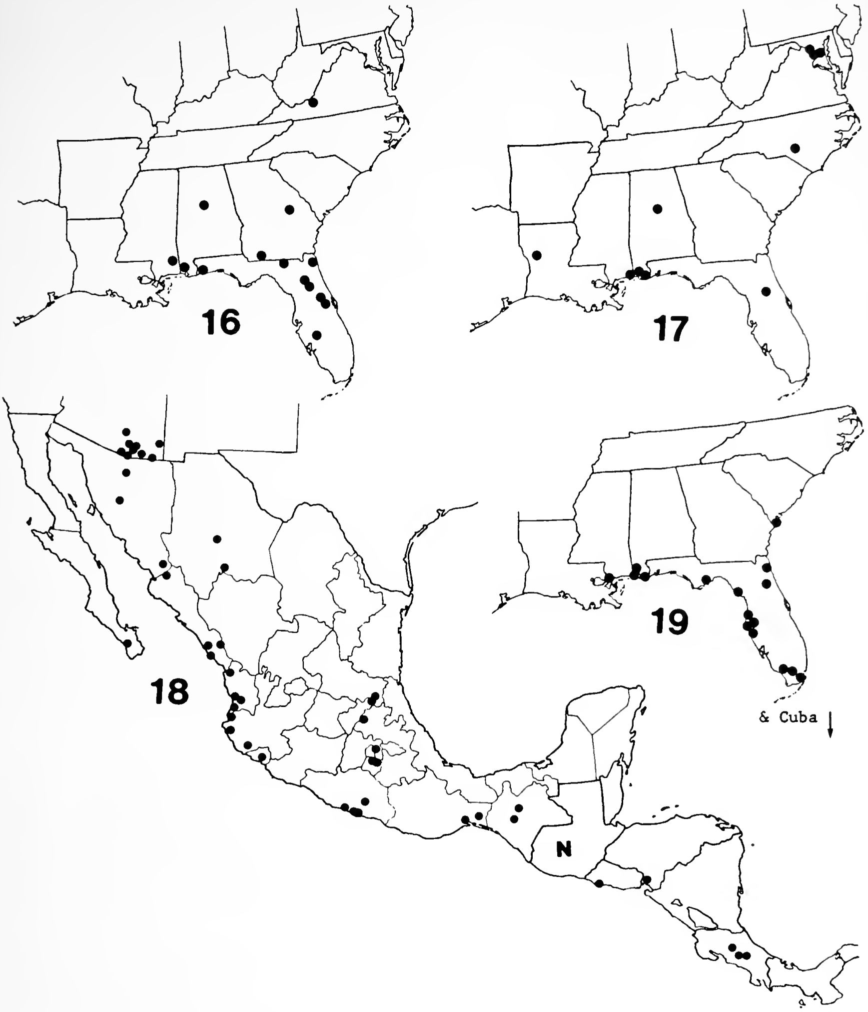
Charidotella was originally proposed as a subgenus of *Metriona* and was based on *Cassida zona* Fabricius, the only originally included species. *Metriona* was proposed in the same paper and, as defined, included nearly all the Cassidini with toothed tarsal claws and hence was a highly artificial assemblage of both New and Old World species. Spaeth (1914) designated *Cassida elatior* Klug as type-species for *Metriona.* This species was originally included and is an excellent example of toothed tarsal claws, the character state originally prescribed for the genus. It is, however, an unusual species possessing a unique combination of features. Considering the contents of "*Metriona*" at the time of Spaeth's 1914 catalog, it was a poor choice for type-species. Spaeth never formally defined *Metriona* nor *Charidotella,* but in an annotated list of Peruvian Cassidinae (1942) he recognized the latter as a full genus with several species listed under it including the common "*Metriona*" *sexpunctata* (Fabricius).

From study of the included species, *Charidotella* is undoubtedly the correct genus for most of the species still cataloged in *Metriona.* It is one of the largest genera of the *Charidotis* Group. Seven species occur in America north of Mexico: *C. emarginata* (Boh.), *C. ormondensis* (Blatchley), *C. purpurata* (Boh.) (these three transferred from *Metriona* to *Charidotella* (*Chaerocassis*) by Hincks (1952, p. 350)), *C. bicolor* (F.), *C. profligata* (Boh.) (here transferred from *Metriona,* NEW COMBINATIONS), and two neotropical species not previously recorded from America north of Mexico. In North America the genus is distributed in southern Canada and throughout the United States. Taxonomy of the North American species and the subgenera listed above are currently under study by the author. Host plants are members of the Convolvulaceae.

Microctenochira Spaeth
Fig. 7

Ctenochira Chapuis, 1875:409 (nec Foerster, 1855).
Microctenochira Spaeth, 1926:36, 104.
Euctenochira Hincks, 1950:509 (new name for *Ctenochira* Chapuis) (subgenus).

Microctenochira (s. str.) *bonvouloiri* (Boheman) occurs from south Texas to Costa Rica and is the only representative of this large neotropical genus that ranges into the United States. It has been collected from *Merrimia dissecta* (Jacq.) Hallier f.



Figs. 16–19. Distributions of North American Cassidini species based on specimens examined by author. 16. *Erepsocassis rubella.* 17. *Opacinota bisignata.* 18. *Metrionella bilimeki.* 19. *Floridocassis repudiata.* N = national record.

(Convolvulaceae) in the area about Brownsville, Texas, and from unidentified Convolvulaceae in Mexico.

GENERA EXCLUDED FROM NORTH AMERICA

Metriona Weise
Fig. 10

Metriona Weise, 1896:13, 14.

In its strict sense, this genus belongs to the *Cassida* Group and is closely related to *Plagiometriona.* It occurs only in South America. The bulk of the species catalogued in *Metriona* belong to *Charidotella* (see discussion under *Charidotella*). Photographs of the type-species, *Cassida elatior* Klug, are provided (Fig. 10).

Nuzonia Spaeth
Fig. 9

Nuzonia Spaeth, 1912:5.
Litocassis Weise, 1921:197.

This generic name entered the North American literature through Blackwelder (1946) who listed *Gratiana* as a junior synonym. The reason behind this synonymy is unknown to the present writer. The apparent synonymy in Blackwelder's catalog was followed in two popular identification manuals (Wilcox, 1954, and Balsbaugh and Hays, 1972) and, excepting Arnett (1968), has been generally adopted. Study of the original descriptions and several representatives of *Gratiana* and *Nuzonia* has shown that both are separate valid genera belonging to the *Cassida* Group. *Gratiana,* whose members are small, pale green, and depressed in body form, has toothed tarsal claws, while *Nuzonia,* whose members closely resemble those of *Coptocycla* (s. str.), has simple claws. Species of *Nuzonia* occur in Central and South America.

During the course of investigating this confusion, a syntype [Spaeth Coll., Manchester Museum] of *Nuzonia ibaguensis* Spaeth, type-species of *Nuzonia,* was examined. The specimen (Fig. 9), a male, labeled "Colombie Ibaque Fr. Claver" "Nuzonia ibaguensis type Spaeth det." "Typus" is here designated as lectotype. A second syntype, a female labeled "Columbia Pehlke," originally deposited in the Stettin Museum and now housed in the Department of Zoology, Agricultural Academy, Wrocław, Poland, is here designated as a paralectotype.

ACKNOWLEDGMENTS

Appreciation is expressed to P. D. Ashlock, University of Kansas [SEMC]; L. Borowiec, Agricultural Academy, Wrocław; Per Lindskog, Riksmuseum Stockholm; and Colin Johnson, Manchester Museum, The University of Manchester, for the loan of primary type material and other specimens required during this work. L. H. Herman, American Museum of Natural History; A. J. Newton, Museum of Comparative Zoology; and R. E. White, United States National Museum, provided loans of much determined and undetermined Cassidini material. Photographs of specimens and SEM work were by G. J. Lenhard and J. G. Aubrey, respectively.

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Received February 27, 1985; accepted June 6, 1985.

J. New York Entomol. Soc. 94(1):115–117, 1986

A NEW SPECIES OF *CARIANCHA* OMAN (HOMOPTERA: CICADELLIDAE: DELTOCEPHALINAE) WITH A DISCUSSION ON THE TRIBAL PLACEMENT OF THE GENUS

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Abstract.—A new species of *Cariancha* Oman is described from Brazil. Evidence is given to support the placement of *Cariancha* in the deltocephaline tribe Acinopterini.

The monotypic genus *Cariancha* was described by Oman in 1936 based on the species *C. cariboba* from Rio de Janeiro, Brazil. Although no tribal placement was indicated with his description of the genus, he placed it in the subfamily Deltocephalinae next to a member of the tribe Euscelini. Later, Evans (1947) placed *Cariancha* in the Euscelini. Metcalf (1967) assigned *Cariancha* to the deltocephaline tribe Goniagnathini. The genus, known only from three females, was treated in the Euscelini by Linnavuori (1959). Oman (1936) and Linnavuori (1959) called attention to the shape of the forewing that was more characteristic of the Acinopterini than of the Euscelini.

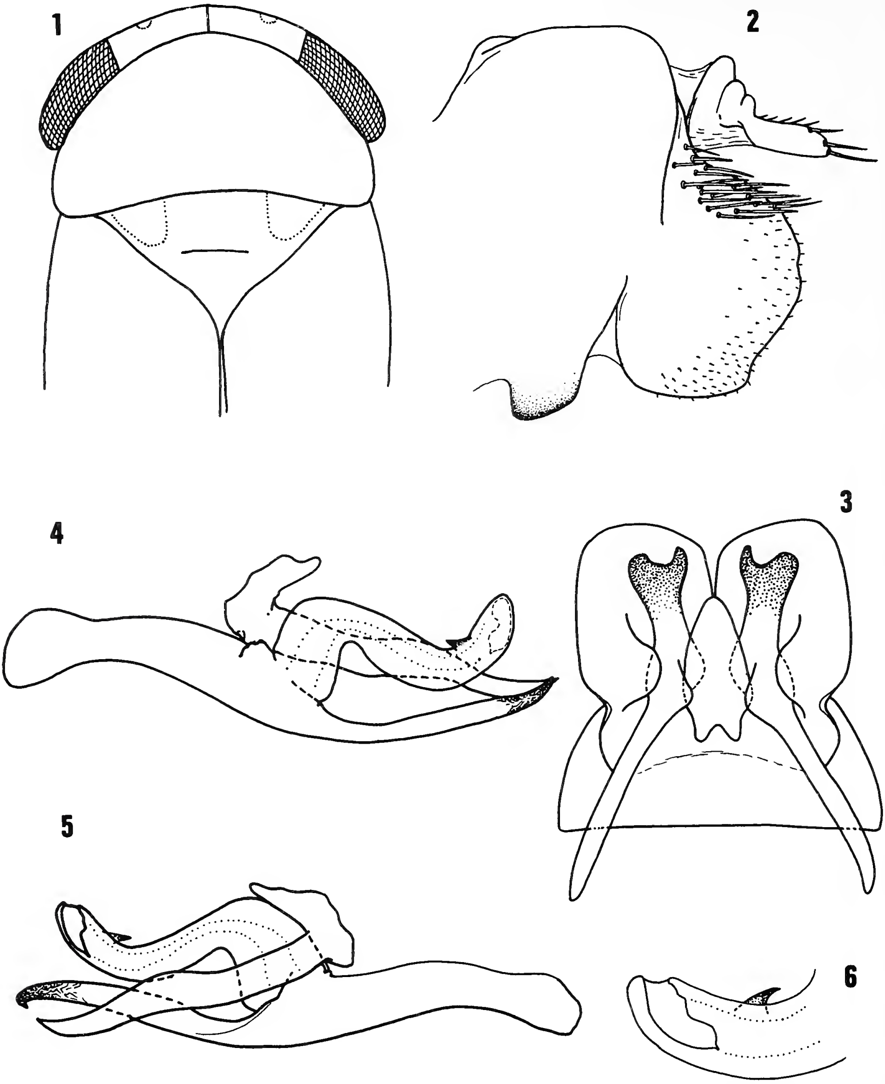
W. D. Fronk, Department of Entomology, Colorado State University, provided a single male Brazilian specimen that matched the general appearance of the holotype of *Cariancha cariboba* Oman. Differences were observed in the overall coloration between the type and the male specimen. Although these differences could be attributed to sexual dimorphism, the male specimen is the same size as the type which is evidence that they are probably not conspecific. Male leafhoppers are usually, but not invariably, smaller than conspecific females.

Although the general body characteristics of *Cariancha* resemble those of the Euscelini, the male genital structures and wing characters indicate closer affinities to the Acinopterini. The simple connective that is plate-like, the forewing that is accuminate apically, the extremely small appendix and the broad face are characteristic of the Acinopterini, not Euscelini. The male plates that are not fused, the forewing not minutely tuberculate and the elongate body separates *Cariancha* from the Goniagnathini.

Cariancha Oman can be separated from *Acinopterus,* the only other genus in the Acinopterini, by having the head slightly wider than the pronotum and the short robust male plates.

Cariancha delongi, new species
Figs. 1–6

Description. Length of male 6.0 mm, female unknown. Medium sized, rather elongate and robust leafhopper. Head slightly wider than pronotum, crown short and



Figs. 1–6. *Cariancha delongi.* 1. Head and thorax, dorsal aspect. 2. Pygofer, left lateral aspect. 3. Plates, valve, styles and connective, dorsal aspect. 4. Aedeagus, left lateral aspect. 5. Aedeagus, right lateral aspect. 6. Apex of aedeagus, right lateral aspect.

broad, uniform length, rounded anteriorly, without microsculpturing. Face broad and short, ocelli about 9× their diameter from eyes, other facial characteristics as in *C. cariboba.* Spinulation of hind tibia 2:2:1.

Color: Crown light brown with two clear round spots laterad to coronal stem, clypellus and posterior half of clypeus dark brown. Pronotum light brown with anterior half irregularly lighter. Scutellum light brown with anterior angles brown.

Forewings brown hyaline, distal portions of claval and radial veins dark brown. Lateral aspect of thorax light brown. Legs light brown with coxae and apex of tibiae dark brown.

Male genitalia: Pygofer with apical half broadly but not smoothly rounded, macrosetae clumped on dorsomedial margin, anal tube somewhat elongate with several macrosetae apically. Plates short and broad, without macrosetae. Valve broadly triangular. Style bifurcated apically. Aedeagus asymmetrical, both aedeagal processes passing on left side of shaft, basal aedeagal processes directed posteriorly in lateral aspect. Shaft compressed with tooth-like process subapically on right side, gonopore apical on right side, shaft curved left in dorsal aspect.

Holotype. ♂—Brazil, M. G. [Minas Gerais], Lavras, 18-X-1978, W. D. Fronk collector; deposited in the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.

Notes. This species is related to *cariboba* Oman but can be separated from it by the lack of a light red band on the margin of the crown. It is named in honor of the late Dwight M. DeLong who encouraged us to work on the leafhopper specimen.

ACKNOWLEDGMENTS

We thank Paul H. Freytag (University of Kentucky) for his comments on the problems of sexual dimorphism as it pertains to leafhopper taxonomy. James P. Kramer (U.S. National Museum) kindly made type material available to the senior author during a recent visit. H. Derrick Blocker (Kansas State University) and Charles A. Triplehorn (The Ohio State University) criticized an earlier draft of this manuscript.

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Received February 15, 1985; accepted July 18, 1985.

J. New York Entomol. Soc. 94(1):118–125, 1986

LIFE HISTORY AND DESCRIPTIONS OF THE IMMATURE STAGES OF THE PLANTHOPPER *STENOCRANUS LAUTUS* (HOMOPTERA: DELPHACIDAE)

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Abstract.—The life history of *Stenocranus lautus* Van Duzee was studied in Missouri from April to November 1984, it was reared in the laboratory and the immature stages were described. *S. lautus* feeds and reproduces on *Carex lurida* Wahl., is bivoltine and apparently overwinters as eggs. Field collected adults kept on potted *C. lurida* in the laboratory laid eggs which hatched and were reared to adults. Durations of the five nymphal stadia were 5.4, 7.5, 16.0, 10.5 and 11.0 days, respectively. Nymphal instars differed in body size, number of pit-like sensoria, development of wingpads, number of metatibial and metatarsal spines, and shape and dentition of metatibial spurs.

Stenocranus lautus Van Duzee has been reported from most of eastern North America, including New Hampshire, New York, Maryland, Washington D.C., Virginia, North Carolina, Illinois and Kansas (Beamer, 1946a; Wilson and McPherson, 1980). *S. lautus* was described by Van Duzee (1897); an illustration of an adult was published by Metcalf (1923) and male genitalic features were described and illustrated by Beamer (1946a). No published information is available on the life history.

As is the case for the majority of planthopper species, very little is known about the life histories of the ca. 60 species of *Stenocranus* (O'Brien and Wilson, in press). Adults and nymphs feed on horsetails (Equisetaceae), grasses (Gramineae), and sedges (Cyperaceae) (Mochida and Okada, 1971). Information on the biology of several Palearctic species has been published. *S. minutus* (Fab.) feeds on *Dactylis glomerata* L. (Gramineae) (May, 1975), is monovoltine (Müller, 1958), overwinters as adults (Ossiannilsson, 1978) and is parasitized by a pipunculid fly (Diptera) (May, 1979). *S. major* (Kirschbaum) feeds on *Phalaris arundinaceae* L. (Gramineae) (Le Quesne, 1960), overwinters as an adult and has been reported as a pest of rice in Italy (Ossiannilsson, 1978). *S. gialovus* Asche and Hoch feeds on *P. aquatica* L. (Asche and Hoch, 1983), *S. matsumurai* Metcalf on *Equisetum arvense* L. (Equisetaceae) and *S. yasumatsui* Ishihara on *Carex* sp. (Cyperaceae) (Lee and Kwon, 1977, 1980).

The present study summarizes the life history of *S. lautus* at Pertle Springs, Johnson County, Missouri, provides information on laboratory rearing, descriptions and illustrations of immature stages and a key to nymphal instars.

MATERIALS AND METHODS

The field study was conducted at Racehorse Lake, Pertle Springs, Warrensburg, Johnson County, Missouri. In an attempt to collect overwintering stages of *S. lautus,* five 10-gallon plastic garbage bags of leaf litter and thatch from in and around the host plants, *Carex lurida* Wahl., were collected on April 15, 1984 and placed in a large modified Berlese funnel. Sweep net samples (50 sweeps/week) were taken twice per week from May 1 to November 15, 1984. The information recorded from these sweep samples included the number of individuals captured, gender of adults, and number of each nymphal instar. Some of the collected individuals were preserved in 70% isopropyl alcohol for measurements and description and some were returned alive to the laboratory for rearing (see below). Potential predators were collected in the field by sweeping and hand picking from the host plants. Feeding and oviposition sites were determined, in both field and laboratory studies, by observing individuals on the host plants.

The laboratory study was begun using an environmental chamber but, because of mechanical failure, the study was conducted in a laboratory where *C. lurida* plants were transplanted from the field site and grown in 16 cm diam. plastic pots. Two fluorescent bulbs on a 16L:8D timer were placed 8–10 cm over the tops of the pots. Room temperature could not be controlled but ranged from ca. 21 to 27°C during the course of the study. Field collected *S. lautus* adults were placed on potted *Carex* and allowed to feed and lay eggs. The insects remained on the plants despite the absence of a cover. After the eggs hatched, the immatures were removed by gently brushing them off the plant with a fine paintbrush and placing them on small, individual *Carex* plants each having 3–4 leaves and planted in 8 cm diam. plastic pots. Both eggs and newly hatched immatures were observed 5–6 times daily.

The information obtained from the laboratory study included number of eggs laid, feeding sites of immatures and adults, number surviving each stage, and length of each stadium. The descriptions and illustrations of the egg and each nymphal instar and a key to nymphal instars are based upon laboratory reared individuals.

The 5th instar is described in detail but only major differences are described for 4th through 1st instars. Measurements are given in mm as mean ± SD. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the body, and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum. Eggs were obtained by removing them from host plants by inserting a needle under each egg and teasing it free.

RESULTS AND DISCUSSION

Field study. No specimens were collected during April and May by either Berlese funnel or sweeping. First, 2nd and 3rd instar nymphs were collected from June 4 to 10; 4th and 5th instar nymphs from June 18 to July 2. Adult males were first collected on June 20 and females on June 25; both sexes were collected through July 25 (Fig. 1). Wax first appeared on the abdomens of females, signaling oviposition, on July 5. Unsuccessful attempts were made to locate eggs in the field. Second generation 1st instar nymphs were collected from August 1 to 6, 2nd from August 1 to 30, 3rd from August 1 to September 8, 4th from August 6 to September 19 and 5th from August 30 to September 21; adults were collected on August 23, but were not collected again until September 19. Wax first appeared on the abdomens of presumed second generation females on October 3. The last adult was collected on October 25 (Fig. 1). *S. lautus* is bivoltine and apparently overwinters as eggs. Evidence to support this

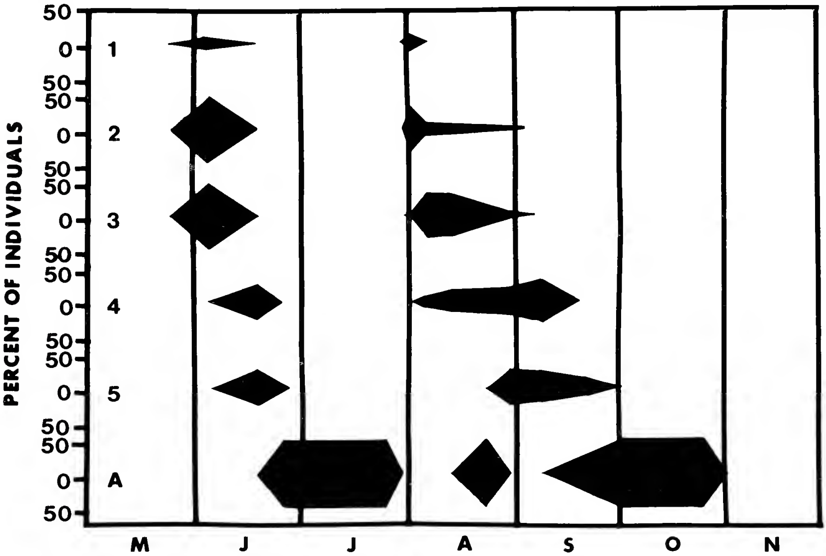

Fig. 1. Seasonal occurrence of *S. lautus* in Missouri. Number of individuals of each stage is expressed as percentage of total individuals of all stages collected per collection date (N_1 = 35, N_2 = 120, N_3 = 166, N_4 = 157, N_5 = 105, N_A = 77).

includes the absence of overwintering adults or immatures in the collected samples, the presence of early instar nymphs in the spring, and the presence of gravid females with oviposition wax in late fall. *S. lautus* differs from other species in the number of generations and overwintering stages. *S. minutus* is monovoltine (Müller, 1958), and *S. minutus* and *S. major* overwinter as adults (May, 1979; Ossiannilsson, 1978).

Feeding sites for adults were not detected in the field but nymphs were observed feeding ca. 4–6 cm above ground level on stems or along the midrib on the underside of leaves.

The spider *Zygoballus bettini* Peckham (Salticidae) was observed feeding on a late instar nymph: 16 other species of spiders, all potential predators collected at the study site are given by Calvert (1985).

Laboratory study. Wax-covered eggs were found inserted singly in horizontal rows on the leaves 9 cm up from the soil. Eggs hatched 16–21 days after being laid. Of 89 eggs laid, 85 hatched but 63 nymphs died during emergence. It took 67 days from the time the first egg was laid until the last adult ecdysis. The 22 surviving nymphs lived for different lengths of time but usually died during ecdysis; 15 died between 1st and 2nd nymphal instar, 3 between 2nd and 3rd, 2 between 3rd and 4th, and only 2 reached adult ecdysis (Table 1). The two individuals that reached adult emerged from their exuvia except for their hind legs; they died in this condition. The length of time from eclosion to ecdysis for these two individuals was 50 days. Durations of the nymphal stadia are given in Table 1. Adults were observed feeding on all emergent parts of the plants, but nymphs were always observed feeding below 7 cm.

Descriptions of nymphal instars. Fifth instar (Fig. 2). Length 2.7 ± 0.31; thoracic length 1.2 ± 0.08; width 1.3 ± 0.10. N = 6.

Table 1. Duration (in days) of the nymphal instars of *S. lautus.*

Nymphal instar	No. beginning	No. completing	Days	
			Range	Mean ± SD
1st	22	7	4–7	5.4 ± 1.3
2nd	7	4	7–8	7.5 ± 0.6
3rd	4	2	15–17	16.0 ± 1.4
4th	2	2	10–11	10.5 ± 0.7
5th	2	2	10–12	11.0 ± 1.4

Body reddish with white middorsal line extending from anterior end of vertex to posterior end of metanotum. Form elongate, subcylindrical, slightly flattened dorsoventrally, widest across mesothoracic wingpads.

Vertex subtriangular; posterior margin almost straight; narrowing anteriorly, lateral margins slightly convex in posterior ⅓. Frons yellowish to brownish with white longitudinal median line; subrectangular; border with clypeus slightly convex; lateral margins convex and carinate (outer carinae) and paralleled by second pair of carinae (inner carinae) which are continuous with lateral margins of vertex; area between inner carinae elevated; region between inner and outer carinae with 9 pits on each side; 8 pits between each outer carina and eye. Clypeus yellowish to brownish, narrowing distally, consisting of subconical basal postclypeus and cylindrical distal anteclypeus. Beak 3-segmented, cylindrical, segment 1 almost entirely hidden by

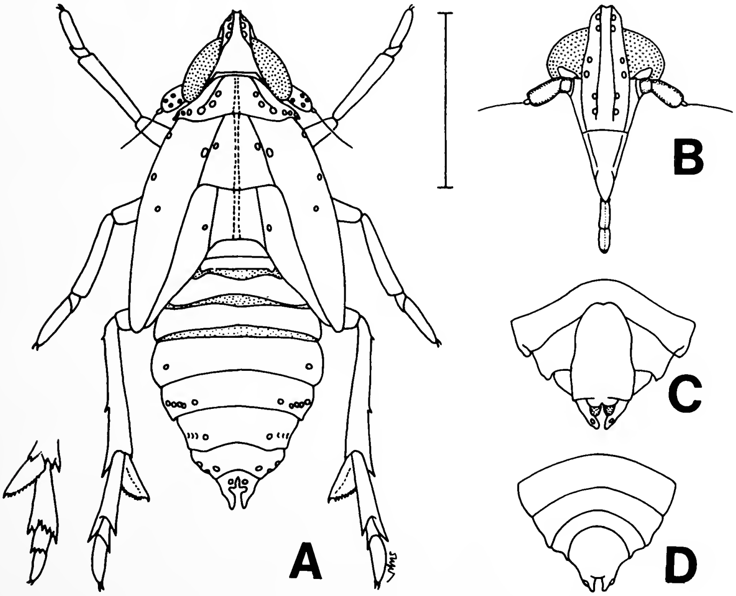

Fig. 2. *S. lautus* fifth instar. A. Habitus. B. Frontal view of head. C. Apical part of venter of female abdomen. D. Apical part of venter of male abdomen. Vertical bar = 1.0 mm.

anteclypeus, segment 2 ca. 1½× length of segment 3, segment 3 with black apex. Antennae 3-segmented; scape short, cylindrical; pedicel subcylindrical, 4× length of scape, with ca. 14–15 pit-like sensoria; flagellum bulbous basally, with elongate, bristle-like extension distally, bulbous base ca. ⅙× length of pedicel. Eyes red.

Thoracic nota divided by middorsal line into three sets of plates. Pronotal plates subtriangular; anterior margin following posterior border of eye, posterior border sinuate; each plate with posterolaterally curving carina originating on anterior margin in median ⅓ and terminating on posterior margin in lateral ⅓; area between carinae elevated and subtriangular; row of 10 pits extending along anterolateral margin of carina to lateral border of plate (lateralmost pits not visible in dorsal view). Mesonotum with median length 1½× that of pronotum; subrectangular; elongate lobate wingpads extending to tips of metanotal wingpads; each plate with posterolaterally directed carina originating on anterior margin in median ¼ and terminating on posterior margin in lateral ½; area between carinae elevated and subtriangular; 2 pits near carina and 3 pits in lateral ⅓. Metanotum with median length ca. 1½× that of mesonotum; subrectangular, lobate wingpads extending to middle of 4th tergite; each plate with posterolaterally directed carina originating on anterior margin in median ¼ and terminating on posterior margin in median ⅓; 1 pit near middle of plate. Pro- and mesocoxae elongate and directed posteromedially; metacoxae fused to sternum. Metatrochanter short and subcylindrical. Pro- and mesofemora and tibia each with 2 ventral longitudinal rows of setae. Metatibia with 2 black-tipped spines on lateral aspect of shaft, an apical transverse row of 5 black-tipped spines on ventral aspect and a subtriangular, flattened movable spur with 12–13 teeth on posterior margin. Pro- and mesotarsi with 2 tarsomeres; tarsomere 1 wedge-shaped; tarsomere 2 subconical, ca. 3× length of tarsomere 1, with pair of apical claws and median membranous pulvillus. Metatarsi with 3 tarsomeres; tarsomere 1 with apical transverse row of 7 black-tipped spines; tarsomere 1 with apical transverse row of 7 black-tipped spines; tarsomere 2 cylindrical, ca. ¼× length of 1, with apical transverse row of 4 black-tipped spines on ventral aspect; tarsomere 3 subconical, ca. 1½× length of 2, with pair of apical claws and median pulvillus.

Abdomen 9 segmented; slightly flattened dorsoventrally, widest across 5th abdominal segment. Tergite 1 small, subtriangular; 2 subrectangular, 2⅓× width of 3; tergites 5–8 each with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): tergite 5 with 1, 6 with 4–5, 7 with 5–6, 8 with 4–5. Segment 9 surrounding anus; with 3 pits; female with 1 pair of acute processes extending from juncture of sternites 8 and 9; males lacking processes.

Fourth instar (Fig. 3E). Length 1.8 ± 0.15; thoracic length 0.7 ± 0.03; width 0.9 ± 0.07. N = 7.

Frons with 7 pits between each outer carina and eye. Antennal pedicel with 9 sensoria; basal flagellum ¼× length of pedicel.

Pronotal plates each with 9 pits. Mesonotal wingpads shorter, covering ca. ⅔ of metanotal wingpad laterally. Metanotal median length subequal to that of mesonotum; carinae weaker; wingpad extending to tergite 3. Metatibial spur slightly smaller with 8–10 teeth on margin. Metatarsi with 2 tarsomeres; tarsomere 1 with apical transverse row of 6 black-tipped spines; tarsomere 2 subconical with 3 black-tipped spines in median portion of tarsomere.

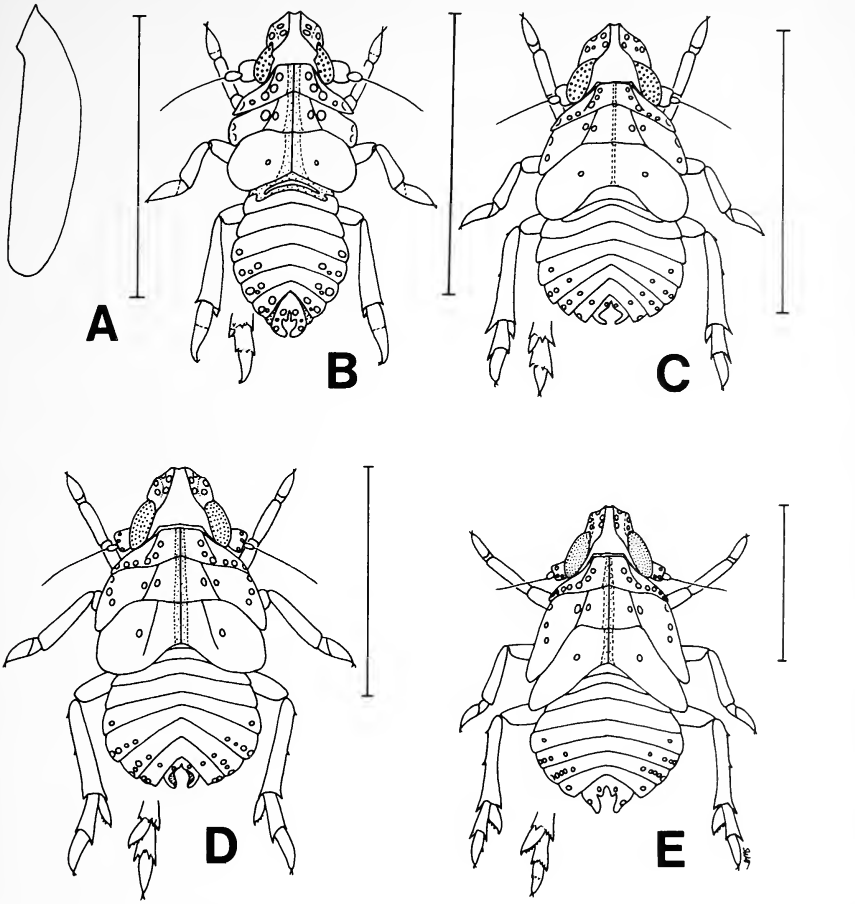

Fig. 3. *S. lautus* immature stages. A. Egg. B. First instar. C. Second instar. D. Third instar. E. Fourth instar. Vertical bar = 1.0 mm.

Abdominal tergites 5–8 with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving on tergites onto ventral aspect): tergite 5 with 1, 6–7 each with 5, 7 with 5, 8 with 3–4.

Third instar (Fig. 3D). Length 1.3 ± 0.11; thoracic length 0.5 ± 0.03; width 0.6 ± 0.04. N = 10.

Frons with 5 pits between each outer carina and eye. Antennal pedicel with 4 sensoria; bulbous base of flagellum ca. 1½× length of pedicel.

Pronotal plates each with 8 pits. Mesonotal wingpad shorter covering ⅓ of metanotal wingpad laterally. Metanotal wingpad extending to juncture of tergites 2 and 3. Metatibial spur smaller; 4 apical teeth on margin. Metatarsomere 1 with apical transverse row of 5 black-tipped spines; tarsomere 2 without spines in middle.

Abdominal tergites 5–8 each with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): tergite 5 with 1, 6–7 each with 4, 8 with 3.

Second instar (Fig. 3C). Length 1.0 ± 0.05; thoracic length 0.4 ± 0.04; width 0.4 ± 0.03. N = 10.

Frons with 3 pits between each outer carina and eye. Antennal pedicel lacking sensoria.

Pronotal plates each with 7 pits. Mesonotal plates each with 4 pits; wingpads undeveloped. Metanotal wingpads undeveloped. Metatibia with apical row of 3 black-tipped spines; spur smaller, ca. 2× length of longest metatibial spine, without marginal teeth, with black-tipped tooth at apex; metatarsomere 1 with 4 apical black-tipped spines.

Abdominal tergite 5 lacking pits, tergites 6–8 each with 3 pits on either side of midline (lateralmost pits not visible in dorsal view due to curving to tergites onto ventral aspect).

First instar (Fig. 3B). Length 0.8 ± 0.06; thoracic length 0.3 ± 0.06; width 0.3 ± 0.02. N = 10.

Bulbous base of antennal flagellum subequal in length to that of pedicel.

Pronotal plates each with 6 pits. Mesonotal plates each with 3 pits. Metanotal plates lacking pits. Metatibia apparently lacking spines on shaft.

Abdominal tergites 6–8 each with 2 pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect).

Egg (Fig. 3A). Length 0.97 ± 0.01; width 0.23 ± 0.01. N = 3.

Eggs laid singly; white; cylindrical flattened, ovoid in anterior ⅕; chorion translucent, smooth.

KEY TO *S. lautus* NYMPHAL INSTARS

1. Metatibial spur with marginal teeth; 5–8 pits between outer carina and eye; pit-like sensoria present on antennal pedicel (Figs. 2, 3D) 2
– Metatibial spur without marginal teeth; 3 pits between each outer carina and eye; antennal pedicel lacking pit-like sensoria; pit absent on abdominal tergite 5 (Fig. 3B, C) 4
2. Metatarsi with 3 tarsomeres; 8 pits between each outer carina and eye; mesonotal wingpads extending to or almost to apex of metanotal wingpads (Fig. 2) ...... 5th Instar
– Metatarsi with 2 tarsomeres (tarsomere 2 may be partially subdivided); 5–7 pits between each outer carina and eye; mesonotal wingpads not extending to apex of metanotal wingpads (Fig. 3D, E) 3
3. Metatarsomere 2 with 3 small spines in middle; 7 pits between each outer carina and eye; mesonotal wingpads covering ca. ⅔ of metanotal wingpads (Fig. 3E) ..... 4th Instar
– Metatarsomere 2 without spines; 5 pits between each outer carina and eye; mesonotal wingpads covering less than ⅔ of metanotal wingpads (Fig. 3D) .... 3rd Instar
4. Metatibia with 2 spines on shaft; abdominal tergites 6–8 each with 3 pits on either side (Fig. 3C) .... 2nd Instar
– Metatibia apparently lacking spines on shaft; abdominal tergites 6–8 each with 2 pits on either side (Fig. 3B) .... 1st Instar

ACKNOWLEDGMENTS

We thank Drs. D. L. Castaner and W. B. Peck, Department of Biology, Central Missouri

State University, Warrensburg, for assistance in identification of the host plant and spiders, respectively. Appreciation is extended to the Office of Graduate Studies for funding this project through a Summer Faculty Development Award to the junior author.

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J. New York Entomol. Soc. 94(1):126–133, 1986

PENTAGRAMMA LONGISTYLATA (HOMOPTERA: DELPHACIDAE): DESCRIPTIONS OF IMMATURE STAGES

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Abstract.—The egg, 3rd, 4th, and 5th nymphal instars, and male and female genitalia of *Pentagramma longistylata* Penner are described and illustrated and an illustration of the adult habitus is provided. Features useful in separating nymphal instars include differences in body and wingpad sizes, spination of metatibiae and tarsomeres, number of metatarsomeres and body pits. *P. longistylata* was collected on *Scirpus americanus* Pers. (Cyperaceae) in Oklahoma and Texas.

Pentagramma longistylata Penner is a little-studied asiracine delphacid known from Florida and Texas (Penner, 1947). Other than Penner's comment that members of this genus are commonly collected on marsh grass, rushes, and sedges, no host plant records have been published.

Little morphological or ecological information is available on the immatures of the approximately 290 species of North American delphacids. Although immatures of Delphacinae (sensu Muir, 1930) have been described, e.g., *Dephacodes bellicosa* Muir and Giffard by Wilson (1985) and *Megamelus davisi* Van Duzee by Wilson and McPherson (1981a), no species of Asiracinae has been described or illustrated. Information on immature asiracines is of interest because adults bear several plesiomorphic features such as the awl-shaped metatibial spur and the aedeagal flagellum. Furthermore, the Asiracinae do not appear to represent a monophyletic group (Asche and Remane, 1982); morphological features of representative asiracine genera may help resolve the status of this group.

This paper presents descriptions and illustrations of the male and female genitalia, egg, and 3rd, 4th, and 5th instar nymphs of *P. longistylata,* compares the nymphs with those of other North American delphacines, and includes comments on some morphological differences between delphacid nymphs and those of certain other planthopper families.

DESCRIPTIONS

Specimens were preserved in 70% ethyl alcohol. The 5th instar is described in detail but only major differences are described for 4th and 3rd instars. Measurements are given in mm as mean ± SD. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the body, and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum. Eggs were obtained by dissecting a gravid female.

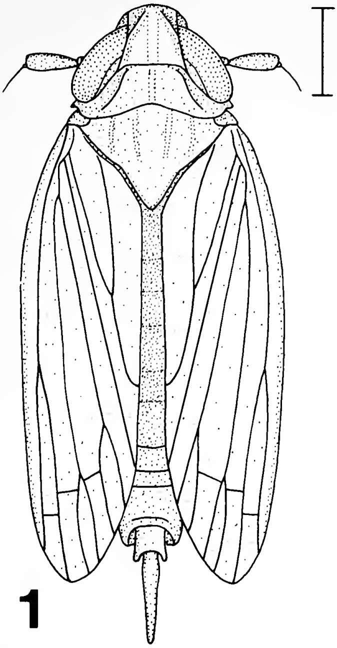


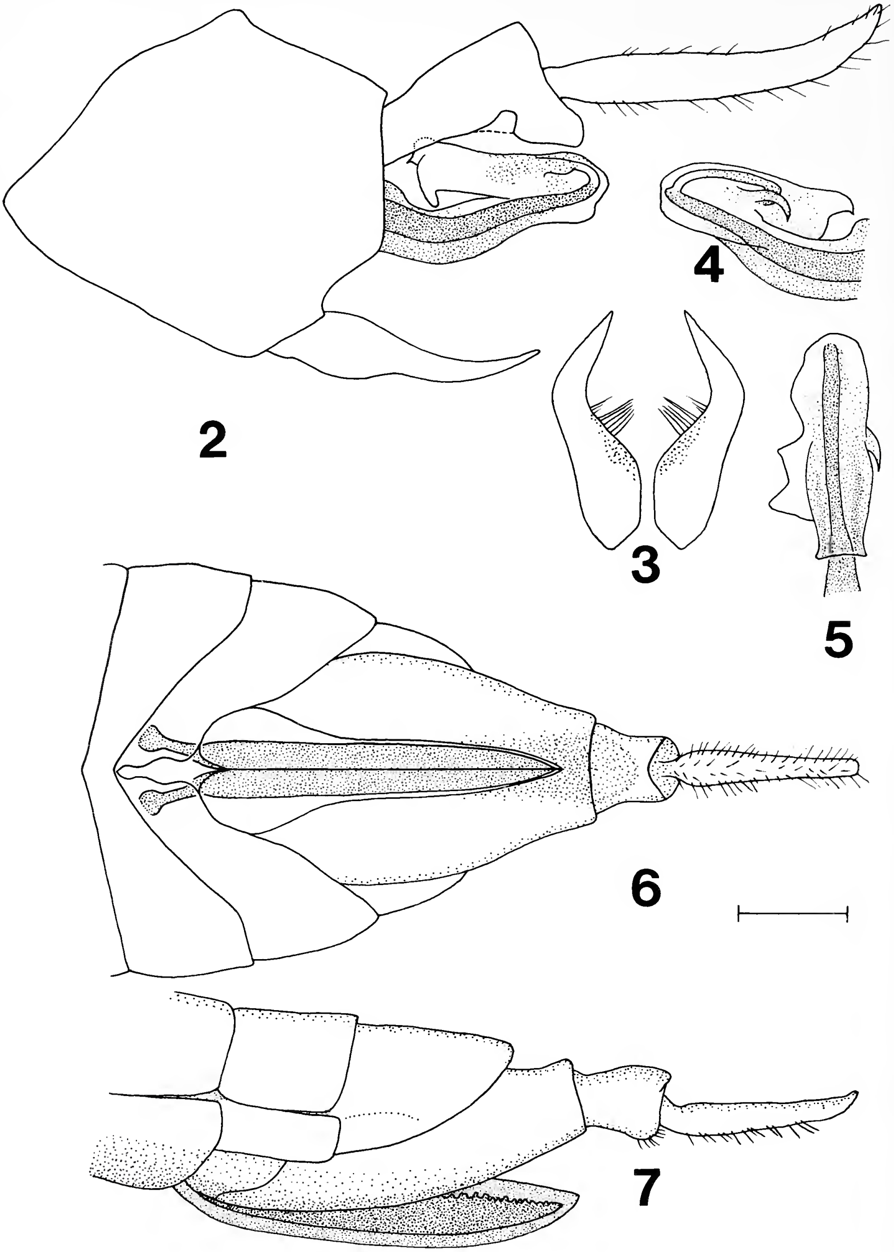
Fig. 1. Habitus of male *Pentagramma longistylata* Penner. Vertical scale = 1.0 mm.

The collecting data for specimens used in the descriptions are: OKLAHOMA: Cleveland Co., S. Canadian River, Norman, Coll. S. Wilson, 3-IX-1978 (2—5th instars, 1♂, 1♀), 29-VIII-1983 (3—3rd, 7—4th, 13—5th, 12♂♂, 9♀♀); TEXAS: Galveston Co., Galveston Isl., 26-IV-1983, Coll. A. G. Wheeler, Jr. (1—3rd, 13—4th, 5—5th, 3♂♂, 3♀♀); all specimens collected on *Scirpus americanus* Pers. (Cyperaceae), commonly known as common three square or American bulrush.

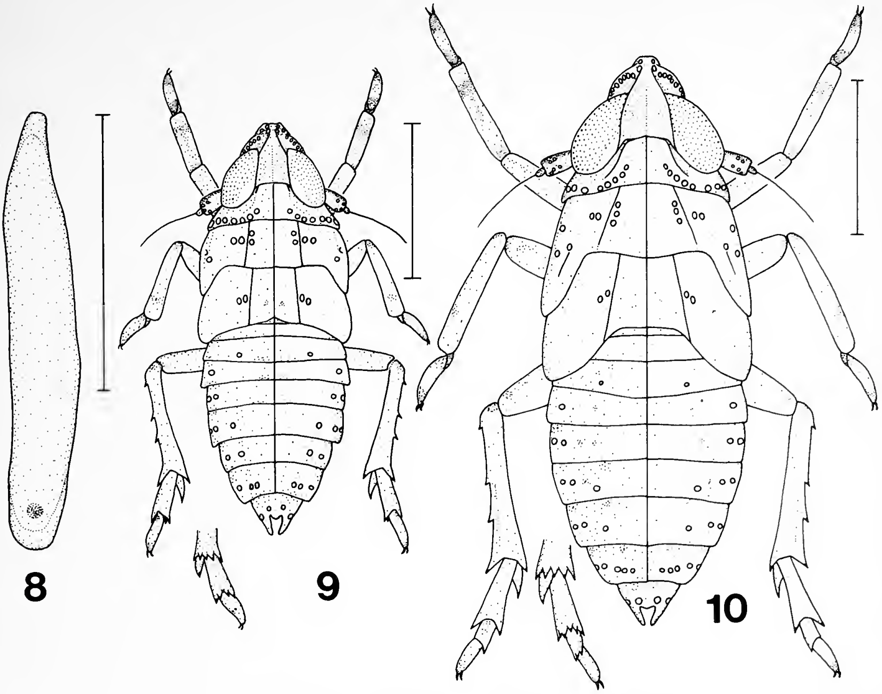
Adult (Figs. 1–7). Penner (1947) provided a detailed description of adult *P. longistylata* and illustrations of the head and pygofer. He did not provide descriptions or illustrations of the details of the male or female genitalia.

Male genitalia (Figs. 2–5). Pygofer cylindrical; caudal edge sinuate in lateral view. Anal tube subcylindrical; in lateral view, with ventral margin produced on either side; anal style elongate, ca. 2 × length of anal tube. Styles caliper-shaped with apices acute, inner margin bearing elongate setae, rugose near middle. Aedeagal complex with basally sclerotized periandrum and apical membranous flagellum folded anteriorly on left side; with internal, heavily sclerotized aedeagus opening distally into slender transparent membranous tube curving anteriorly and opening into flagellum; flagellum bearing a curved, acute process on right side.

Female genitalia (Figs. 6, 7). Segment 9 elongate, subcylindrical with a deep sternal, longitudinal groove for reception of the valvulae. Anal tube cylindrical, length subequal to width; anal style slender, elongate, 2–2½× length of anal tube. Valvulae 3 (sawcase) lanceolate, broadest in basal ⅓. Valvulae 2 lanceolate, convex, and ex-



Figs. 2–7. *P. longistylata* male and female genitalia. 2. Complete left lateral view of male. 3. Styles. 4. Aedeagus, right lateral view. 5. Aedeagus, ventral view. 6. Ventral view of female. 7. Left lateral view of female. Vertical scale = 0.5 mm.



Figs. 8–10. Immature stages of *P. longistylata*. 8. Egg. 9. Third instar. 10. Fourth instar. Vertical scales = 1.0 mm.

tending to apex of valvulae 1. Valvulae 1 thick, fused medially for most of length, lateral edges curved over onto dorsal aspect creating troughlike appearance, ventral aspect with a longitudinal row of well-developed teeth in distal ⅔.

Fifth instar (Figs. 11–14). Length 4.1 ± 0.34; thoracic length 1.3 ± 0.09; width 1.5 ± 0.13 (N = 18).

Form elongate, subcylindrical, slightly flattened dorsoventrally, widest across mesothoracic wingpads. Body pale green in life (whitish in alcohol) with reddish and white transverse markings on head and fuscous longitudinal stripes on antennae and pro- and mesothoracic legs.

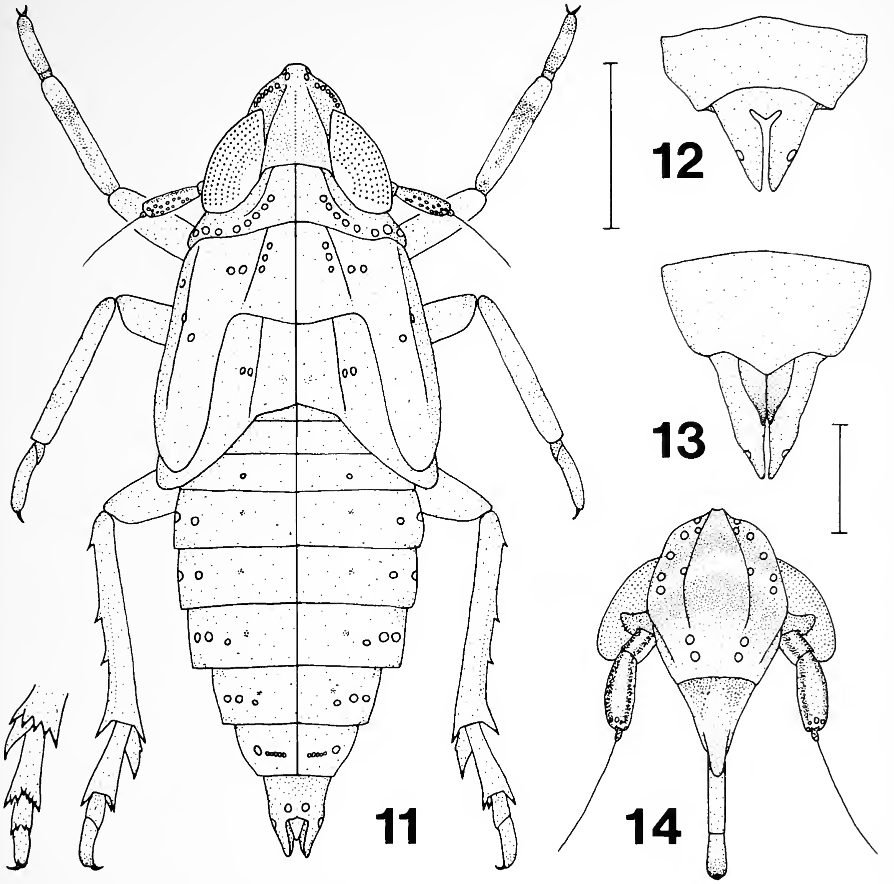
Vertex subtriangular, length subequal to width, lateral margins carinate, extending onto frons as inner carinae. Frons green with 2 orange transverse bands, 1 in upper ⅓, the other in lower ½, separated by transverse white band extending onto genae, a white band at frontoclypeal juncture; ovoid, slightly longer than wide; lateral margins carinate (outer carinae), extending from juncture of vertex to clypeal border and parallel pair of inner carinae; 11 pits between each outer and inner carina, 7–8 pits between each outer carina and eye. Clypeus narrowing distally, consisting of subconical basal postclypeus and cylindrical distal anteclypeus. Beak 3-segmented, segment 1 obscured by anteclypeus, segment 2 1½× length of segment 3. Eyes red with white stripes. Antennae 3-segmented, scape and pedicel subcylindrical, with a pair of longitudinal brown stripes on anterior aspect; pedicel ca. 2× length of scape, with more than 25 pitlike sensoria; flagellum bulbous basally, filamentous distally, basal portion ca. ⅑ length of pedicel.

Thoracic nota divided by middorsal line into 3 pairs of plates. Pronotum with each plate subrectangular, anterior margin following curvature of posterior border of eye, posterior margin slightly sinuate; each plate with a lateral carina in median ⅓ of pronotum extending from anterior margin posterolaterally curving outwards and disappearing in posterior ⅓ of plate, carina bordered along inner margin by a row of 12 pits extending posterolaterally to lateral border of plate (lateralmost pits not visible in dorsal view). Mesonotum with median length ca. 1.3× that of pronotum; each plate bearing an elongate, lobate wingpad extending to near apex of metanotal wingpad; with longitudinal carina originating in median ⅓ and extending posterolaterally to near posterior border of plate; with a row of 3 pits along inner margin of carina and 2 pits between carina and lateral margin of plate; with an outer partial longitudinal carina in lateral ¼ originating near anterior border of plate and disappearing on wingpad; with 3 pits near outer carina. Metanotum with median length subequal to mesonotum; each plate with weak longitudinal carina in median ⅓; wingpad lobate, extending just beyond juncture of 3rd and 4th abdominal tergites; with 2 pits lateral to carina. Pro- and mesocoxae elongate, posteromedially directed; procoxae with dark markings on ventral aspect, metacoxae fused to metasternum. Metatrochanters globose with minute teeth on medial margins. Pro- and mesofemora with longitudinal brown stripes; metafemora with a partial longitudinal brown stripe. Protibiae with longitudinal brown stripes and a transverse brown stripe in distal ½. Metatibiae with 3 black-tipped teeth on lateral aspect of shaft and an apical transverse row of 5 black-tipped spines on ventral aspect, with a conical, moveable black-tipped spur 2× or more length of longest tibial spine. Pro- and mesotarsi each with 2 tarsomeres; tarsomere 1 wedge-shaped, tarsomere 2 elongate, subcylindrical and curved; tarsomeres of prothoracic legs with dark brown transverse stripes or entirely dark brown, mesothoracic tarsomeres similar but lighter; metatarsi with 3 tarsomeres, tarsomere 1 with an apical transverse row of 8 black-tipped spines on ventral aspect, tarsomere 2 ca. ½× length of 1, with an apical transverse row of 4 black-tipped spines on ventral aspect, tarsomere 3 similar but shorter than terminal tarsomeres of other legs; all tarsomeres bearing a pair of brown, curved apical claws and a median membranous pulvillus.

Abdomen 9-segmented, slightly flattened dorsoventrally, widest across segment 4. Tergite 1 very small, tergites 2–9 each with a weak median longitudinal carina; 3–8 each with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): 3 with 1, 4 with 2, 5 with 3, 6 with 5, 7 with 5, 8 with 8. Segment 9 cylindrical, with 3 pits on either side of midline; females with 1 pair of acute processes extending from juncture of sternites 8 and 9; males lacking processes.

Fourth instar (Fig. 10). Length 2.8 ± 0.29; thoracic length 0.9 ± 0.03; width 1.0 ± 0.05 (N = 20).

Vertex slightly longer than wide. Frons with width ¾× length; 11–12 pits between each inner and outer carina and 6–8 pits between each outer carina and eye. Antennal flagellum with bulbous portion ca. ⅕ length of pedicel; ca. 13 pitlike sensoria on pedicel.



Figs. 11–14. *P. longistylata* fifth instar. 11. Nymph. 12. Male, ventral view of apex of abdomen. 13. Female, ventral view of apex of abdomen. 14. Head, frontal view. Vertical scales = 1.0 mm (11); 0.5 mm (12–14).

Pronotum with 10–11 pits on each plate. Mesonotal wingpads shorter, covering ca. ½ of metanotal wingpads laterally. Metanotum with median length slightly longer than that of mesonotum; wingpads extending to tergite 3. Metatarsi with tarsomere 1 bearing 7 apical black-tipped spines on ventral aspect; tarsomere 2 with an apical row of 3–4 black-tipped spines on ventral aspect, middle spines very weak.

Abdominal tergites with the following pits on either side of midline: tergite 3 with 1, 4 with 2, 5 with 4–5, 6 with 4–6, 7 with 6–7, 8 with 8–10. Segment 9 with 3 pits on either side of midline. Females with lobate processes at juncture of sternites 8 and 9 very small.

Third instar (Fig. 9). Length 2.0 ± 0.09; thoracic length 0.7 ± 0.04; width 0.7 ± 0.06 (N = 4).

Vertex with length ca. 1½× width. Frons with 10–11 pits between each inner and outer carina and 6 pits between each outer carina and eye. Antenna with pedicel bearing ca. 5 pits.

Pronotum with 9 pits on each plate. Mesonotal wingpads shorter, covering ca. ⅓ of metanotal wingpads laterally. Metatarsi with 2 tarsomeres, tarsomere 1 with an apical transverse row of 5 black-tipped spines; tarsomere 2 similar to terminal tarsomeres of later instars, occasionally with 1–2 very tiny black-tipped teeth on ventral aspect near middle.

Abdominal tergites with the following number of pits on either side of midline: 3 with 1, 4 with 2, 5 with 4, 6 with 5, 7 with 5, 8 with 6. Segment 9 with 3 pits on either side of midline. Lobate processes originating from sternite 8 of female apparently lacking.

Egg (Fig. 8). Length 1.2 ± 0.03; width 0.2 ± 0.02 (N = 10).

Elongate, cylindrical, slightly sinuately curved; narrowing at ends; anterior end somewhat truncate, posterior end broadly rounded. Chorion translucent, with very small shallow pits (not illustrated), white.

NOTES ON MORPHOLOGY

Pentagramma nymphs differ from those of delphacines examined (e.g., *M. davisi, D. bellicosa*) in the larger number of antennal sensoria present in each nymphal instar, the presence of dorsal median longitudinal carinae on the abdominal tergites, and in the number of metatarsomeres in the 4th instar. In 4th instar nymphs of acanaloniid, cixiid, flatid, issid, and tropiduchid planthoppers there are 3 well-defined metatarsomeres (Wilson and McPherson, 1981b–d; Wilson and Tsai, 1982; Wilson et al., 1983; Wilson and Wheeler, 1984). Fourth instar delphacines have a partial subdivision of the terminal (2nd) metatarsomere with 2 weakly developed teeth on the ventral aspect (Metcalfe, 1969; Wilson and McPherson, 1981a; Wilson, 1985). The 3 well-defined tarsomeres with 3–4 terminal teeth represent a plesiomorphic condition within the Delphacidae. This condition also has been found in 4th instars of Old World asiracines (Asche, Hoch, and Remane, pers. comm.).

ACKNOWLEDGMENTS

We thank Dr. D. L. Castaner, Department of Biology, Central Missouri State University, Warrensburg, for identifying the host plant and Dr. R. Remane, Mr. M. Asche, and Ms. H. Hoch, Fachbereich Biologie-Zoologie, Philipps Universität, Marburg, West Germany, for providing information on asiracine phylogeny.

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Received June 5, 1985; accepted July 18, 1985.

BOOK REVIEW

J. New York Entomol. Soc. 94(1):134–136, 1986

Insect Communication.—Trevor Lewis (ed.). 1984. 12th Symposium of the Royal Entomological Society of London. September 7–9, 1983. Academic Press, Inc., Orlando, Florida. i–xvii, 414 pp. $55.00 (cloth).

"There are more than one million species of insects living on earth. They not only comprise the largest amount of animal biomass in most terrestrial habitats, but also exhibit the greatest diversity of social organizations in the animal kingdom. It is not surprising, therefore, that in no other animal class do we find communication behavior nearly so diversified as in the Insecta" (p. 350). This passage by Hölldobler gives an indication of the variety, complexity and sheer volume of material that could legitimately be included in a volume entitled *Insect Communication.* The 16 chapters and remarks by Professor Sir Richard Southwood which make up this volume are the product of the 12th Symposium of the Royal Entomological Society of London, celebrating the 150th year of its foundation. Unlike many symposium volumes, in which the individual chapters may seem only tenuously related to a central theme, *Insect Communication* gives a well rounded and well organized picture of current research and potential future advances in the study of insect communication, with a minimum of overlap between chapters.

The first chapter by the volume's editor, Trevor Lewis, sets the stage for the following authors by defining communication and then discussing potentially productive or provocative areas for future research. These include the production and perception of pheromone blends, the use of insect communication channels in biological control of insect pests, and electromagnetic communication, including the controversial proposal by Callahan that pheromone perception is partly, if not primarily, electromagnetic in nature.

Five chapters deal primarily with a single sensory modality. In their chapter on visual acuity in arthropod eyes Wehner and Srinivasan compare single lens and compound eyes, and the visual world of insects and salticid spiders. H. C. Bennet-Clark discusses insect hearing; the approach used in this chapter is to treat hearing as a physical system, from sound production and transduction to adequate stimulus of sensory cells, peripheral neural response and central nervous system coding mechanisms. Although the author claims to make no pretense of completeness in his coverage, this chapter is an excellent summary of a large and complex field. Ewing's chapter on acoustic signals in insect sexual behavior is complementary to Bennet-Clark's, focusing on the mechanisms of sound production and their uses in courtship. The chapters by Boeckh ("Neurophysiological Aspects of Insect Olfaction") and Silverstein ("Chemistry of Insect Olfaction") are also complementary, covering as their titles suggest, the structure and functioning of chemoreceptors and of pheromones. The chapter by Silverstein also includes a critical discussion of methodology in the collection, identification and bioassaying of pheromones.

The remaining chapters discuss the role of communication in specific taxa or in specific contexts. Four of these chapters concentrate primarily, though not exclusively, on the uses of chemical communication. Borden summarizes research on colonization, aggregation and dispersal of the Mountain Pine beetle (*Dendroctonus ponderosae*), the Elm Bark beetles (*Scolytus scolytus* and *S. multistriatus*) and three Ambrosia beetles (*Trypodendron lineatum, Gnathotrichus sulcatus* and *G. retusus*). Howse discusses the interaction of nest structure, foraging habits and chemical defense against predators among the social insects. He identifies several "strategies" in defense; for example those species which invest heavily (in terms of energy) in nest construction and large brood tend to show vigorous defense of their investment against predators, while species with "low cost" nests and small standing crop of brood may disperse (when attacked) and later regroup. Morgan discusses the use of chemical communication in foraging and recruitment in social insects, particularly the ants, and Cardé and Charleton summarize the use of olfactory communication in lepidopteran mating systems. Rather than dwell on the steadily growing catalogue of lepidopteran pheromones, they concentrate on searching strategy, orientation to pheromones emitted by flying moths, and the problem of maintaining a selective response to a particular blend of pheromones when the composition of the mixture may vary with distance from the source of emission and with atmospheric conditions. The chapter by Case on vision in the mating behavior of fireflies covers the physiological adaptations of firefly eyes for the detection of light signals, and summarizes the signalling strategies of species that signal solitarily and those that routinely engage in synchronous signalling. Most satisfying is a proposed mechanism for the evolution of synchronized flashing which relies on individual selection. Koeniger presents an interesting, tightly focused chapter on experimental study of the factors important for recognition and proper care of pupae by the honey bee, *Apis mellifera* and the hornet, *Vespa crabro.*

The final four chapters of the volume discuss the role of communication in higher level biological contexts. Probably the most controversial of these chapters is West-Eberhard's "Sexual Selection, Competitive Communication and Species-Specific Signals in Insects." The central tenet is that the variety observed in courtship ritual, male external genitalia, etc., evolved primarily as the result of sexual selection, not as a result of selection for species isolating mechanisms. While this alone may not seem particularly heterodox, some of the ramifications of this idea are sure to generate discussion: e.g., that rapid signal evolution under sexual selection may be important in insect speciation; or the continuing action of sexual selection in the absence of heritable variation in the trait under selection. "How Parasites Locate Their Hosts; a Case of Insect Espionage" by Vinson brings a variety of approaches to bear on the analysis of host-finding by parasites. These include the nature of the stimulus used by the parasite to detect potential hosts, the role of spatial distribution of the hosts and the host's habitat on selection strategy, the use of kairomones to detect the host, and the behavior of the parasite and the defenses of the host. In the chapter "Evolution of Insect Communication" Hölldobler first gives an overview of the role of communication in insect reproduction, in particular its role in reproductive isolation and mate choice. This short summary provides a good background for West-Eberhard's arguments. Hölldobler then goes on to discuss the role of communication in recognition (in particular, kin recognition) and maintenance of dominance in social insects, and functioning and evolution of recruitment signals in Hymenoptera. In the chapter on the exploitation of insect communication by humans, Wall focuses on the feasibility of using pheromones and other chemical signals in the biocontrol of insect pests, by both suppression of pest populations and improvement of the efficiency of conventional pesticides.

Overall this is a fine work and an excellent introduction to the subject of insect communication for those not primarily engaged in communications research. The lists of references at the end of each chapter provide a convenient point of departure for more detailed reading in particular areas. The weaknesses of the book are relatively minor: The index lists pheromones mentioned in the text and common and scientific names of taxa, but does not index subject matter well; the numerous typographical errors are at most annoying, and sometimes amusing, as in the case of the firefly *Pteroptyx cribellata,* which synchronizes its flashes with competing conspecific males "by a simpleresent mechanism"; I suppose I'd resent it too.—*Deborah R. Smith, Michigan Society of Fellows and Museum of Zoology, Insect Division, University of Michigan, Ann Arbor, Michigan 48109.*

INSTRUCTIONS TO AUTHORS

The *Journal of the New York Entomological Society* is devoted to the advancement and dissemination of knowledge of insects and related taxa. The costs of publishing the Journal are paid by subscriptions, membership dues, page charges, and the proceeds from an endowment established with bequests from the late C. P. Alexander and Patricia Vaurie. The Journal will consider for publication manuscripts of any length dealing with original research in entomology. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

Manuscripts should be submitted in duplicate to: Dr. Randall T. Schuh, Editor, Journal of the New York Entomological Society, c/o Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. All material must be double-spaced (including references, tables, captions, etc.) and prepared in the format of a recent issue of the Journal.

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Journal of the New York Entomological Society

VOLUME 94 JANUARY 1986 NO. 1

CONTENTS

Book Review

Vol. 94 APRIL 1986 No. 2

Journal
of the
New York Entomological Society

(ISSN 0028-7199)

Devoted to Entomology in General

JOURNAL OF THE NEW YORK ENTOMOLOGICAL SOCIETY

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Incorporating The Brooklyn Entomological Society

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Meetings of the Society are held on the third Tuesday of each month (except June through September) at 8 p.m. in the American Museum of Natural History, Central Park West at 79th Street, New York, New York.

Mailed April 8, 1986

The Journal of the New York Entomological Society (ISSN 0028-7199) is published quarterly (January, April, July, October) for the Society by Allen Press, Inc., 1041 New Hampshire, Lawrence, Kansas 66044. Second class postage paid at New Brunswick, New Jersey and at additional mailing office.

Known office of publication: American Museum of Natural History, New York, New York 10024.

Journal of the New York Entomological Society, total copies printed 850, paid circulation 700, mail subscription 700, free distribution by mail 18, total distribution 718, 132 copies left over each quarter.

CONTRIBUTIONS ON

HETEROPTERA

In Honor of the Seventieth Birthday of

Richard C. Froeschner

Edited by
THOMAS J. HENRY
AND
ALFRED G. WHEELER, JR.

FOREWORD

Despite his many responsibilities he was never too busy to help others.

W. J. Knight in eulogizing the British hemipterist W. E. China (Ent. Mon. Mag. 115: 165, 1980)

On a weekend collecting trip in summer 1984, we were discussing Dick Froeschner's career, acknowledging not only his influence on hemipterology but marveling at his willingness to help others and his boundless enthusiasm and good cheer. Somehow the subject of his age came up—yes, he had to be in his late 60's—and we immediately thought of doing something special in honor of his 70th birthday. An issue of some entomological journal dedicated to that notable occasion seemed appropriate.

Dick has helped heteropterists throughout the world, and many would admit to having been influenced by his thinking and encouragement. He has been candid with advice and has shared freely his vast knowledge of the group. His impact on many younger workers has been crucial. That he is held in high esteem by his colleagues is evidenced by the dedicatory statements contained in this issue.

We are grateful to the worldwide group of heteropterists who accepted our invitation to share in honoring Dick Froeschner. His wife and brothers and an admiring former student kindly provided articles giving insight into Dick as a young naturalist and detailing the development of a fruitful career in teaching and research. To Randall Schuh, editor of the *Journal of the New York Entomological Society*, we owe special thanks for valuable editorial assistance and for allowing a summertime dream of a "Festschrift" to become reality.

Thomas J. Henry and A. G. Wheeler, Jr.

J. New York Entomol. Soc. 94(2):137–140, 1986

RICHARD C. FROESCHNER: A WIFE'S VIEW

Elsie Herbold Froeschner

When Tom Henry and Al Wheeler asked me to write a paper for this volume honoring Dick, I wondered how I could describe in a few pages the many years of collaboration and forty-five years of marriage to someone I consider a fine scientist, philosopher, distinguished teacher, semanticist, and man of high standards, but also one who can relate to the everyday world.

The time is 1938–39, my first year as medical and biological artist at the University of Missouri. A friend, an odonatologist from my Alma Mater, the University of Michigan, came to visit and to use the insect study collection. After a few day's work at the Entomology Department, she told me of a very knowledgeable young entomologist who had been studying insects since he was ten years old. After a field trip with this man, she remarked I should go out with him and learn about the local fauna and flora, especially the insects! That was my first knowledge of Richard Charles Froeschner.

Since I was responsible for research illustration in seven departments, I did not get near the Entomology Department for months. Finally, an assignment to illustrate a piece of inflamed throat tissue from a cow with a bot warble fly infestation brought me to work there. Quite casually I met Dick. It was the beginning of our long and loving association.

Dick's college career began in 1937 because of a Miss Mary McCarty, a high school science teacher, who believed in him and his ability so much that she volunteered, in the midst of the Depression, to drive him to the University of Missouri, pay his entrance fees, buy books, and give him money for room and board for one month. Mind you, this was a loan, not a gift.

Soon after beginning undergraduate work, Dick began to envision a study of the Hemiptera of Missouri. Already familiar with the midwestern Hemiptera and their ranges, he soon was projecting what should be found in the state. However, much survey work was needed. He had an old Model A Ford and with gas 10¢ a gallon (yes it really was), we started collecting. Dick soon realized that he needed many illustrations for the planned publication. He could do them, but his studies didn't allow the time, and because he had only $15.00 a month for room and board, he couldn't hire them done. By this time, I believed in him and his work so firmly that I volunteered to contribute some pen and ink drawings to be done at night and on weekends. We spent many hours on this project when he wasn't engaged in his studies and I in my daily illustration work.

These common interests deepened our friendship and we were married in 1940, the same year that Part I of the Hemiptera of Missouri was published. Following his B.S. degree, Dick worked as assistant to the State Entomologist of Missouri and then in 1943 became the state representative on a project dealing with the introduced scale insect *Parlatoria chinensis* in St. Louis. He continued work on the Hemiptera of Missouri, and I worked on drawings for the next sections.

Fig. 1. Dick and Elsie Froeschner collecti~~on~~ing in Franklin County, Missouri, Spring, 1943.

In 1944 our first daughter Ellen was born. World War II was in progress and shortly Dick was drafted. He served as Chief Ward Master at an army hospital in Florida. Later, while stationed in Utah, he was about to be sent to Washington to work on insect projects when the war ended.

Returning to St. Louis in 1946, he became Chief Curator and Head of the Science Museum of the St. Louis Academy of Sciences housed in a good-sized mansion. He planned all sorts of programs, exhibits, and wrote detailed descriptions of all the artifacts in a clear, lucid style. I painted the backgrounds of the cases, printed signs, and generally helped with exhibits. Dick collaborated in writing a paper on man's early flight, touching on Montgolfier's balloons and other examples of man's attempt at flight.

By now he had published Parts II (1942) and III (1944) of the Hemiptera series and papers on the Cercopidae, Cicadidae, Erotylidae, Languriidae, and Neuroptera of Missouri. In 1948, Dick received an invitation from Dr. Joseph Bequaert at the Museum of Comparative Zoology at Harvard University to work on their Hemiptera collection. With a new baby daughter Kay added to the family, Dick built a platform for the back seat of our car, converted it to a comfortable play pen for Ellen and Kay, and we traveled east to Cambridge, Massachusetts for three months.

Graduate school soon beckoned at Iowa State College (now University). Drs. Carl Drake, Harry Knight, and Halbert Harris encouraged Dick to get his advanced degrees. He began by working on the grasshoppers and other Orthoptera of Iowa for his Master's thesis. I happily contributed more than 120 pen and ink drawings.

For his Ph.D., he returned to the Hemiptera with a monograph of the "Cydnidae of the Western Hemipshere." Published by the Smithsonian Press, this work may have been the first step toward our later association with the Smithsonian Institution's National Museum of Natural History in Washington, D.C.

During our stay at Iowa State, we enjoyed many Saturday nights at the home of his adviser Dr. Harry Knight and his wife Jessie. There we watched television (it

Fig. 2. Dick Froeschner in his office, Smithsonian Institution, 1986.

would be years before we had a TV), often in the company of José Carvalho, a fellow graduate student and hemipterist, and his wife Milza. We also become acquainted with other grad students working on Hemiptera—Leonard Kelton, Joseph Schaffner, and James Slater. The wives in this close-knit department formed a social club known as "The Grubs" and organized picnics and other outings.

As a new Ph.D., Dick became Assistant Professor of Zoology and Entomology at Montana State College at Bozeman, where our family spent some happy years. Dick taught beginning zoology, general entomology, systematic entomology, and advised graduate students. That he was an excellent teacher was demonstrated in 1958 when he was voted distinguished Teacher of the Year by a faculty committee, a college board group, and student committee. The award was both a certificate of honor, plus a cash award. His department head, Dr. James Pepper, stated that "Dr. Froeschner is a natural born teacher and his first interest is always the student. His teaching is by no means confined to the class room as he is always helping students, whether or not they are in his particular classes." He was very popular with students, as he lectured clearly and concisely and illustrated his lectures with spontaneous chalk drawings on the blackboard. They loved the mice he drew to illustrate problems in genetics. He prodded them to think, and think, and think again. Often Dick and his students would hold heated debates on many subjects, including one on infinity to which even physics graduate students came. Dick often took one side of a question, argued it, and suddenly reversed his stand, forcing the students to reverse their thinking. The students who engaged in these sessions enjoyed them—I believe it made them sharpen their thinking powers.

The workload of over thirty classroom hours in lecture and laboratories did not leave much time for his own research on Hemiptera. He did, however, manage to work on building the college insect collection and somehow found time to go on many field trips with his students. Eventually though, with some regret, he decided to leave teaching to devote his time to research in Hemiptera.

In 1960 he accepted a position as Hemipterist with the Systematic Entomology Laboratory staff at the Department of Agriculture in Washington, D.C. A little disappointed there, he returned to teaching entomology at the University of Montana for a year, followed by a summer session at the University of Montana Biological Station. He was fortunate to get a special group of students who becamed so enthusiastic that they began all night studying marathons, with various kinds of background music to help keep them awake. For our family, wonderful field trips in that beautiful mountain country made that summer a most memorable one.

In the fall of 1962, Dr. J. F. Gates Clarke, then Chairman of the Department of Entomology at the Smithsonian Institution, asked Dick to join the staff in the Department as Curator of Hemiptera, which he did so with enthusiasm. Some people might say he is happy as a clam but perhaps more appropriate to his work, I would say he is as happy "as a bug in a rug."

Lest you think all his waking hours are concerned with Hemiptera, one activity that has been a yearly highlight in our family since Ellen's first Christmas is the creation of a new Christmas scene for under our tree. The scenes are about 3 feet wide and 1.5 feet deep. Dick and I designed each one—he carved the wooden figures up to 6 inches tall, I painted and dressed them, he mechanized them with motors under the stage, I painted the scenery, and by our collaboration, we turned out beautiful scenes, some even of bugs (mostly of the "lady bug" variety, however). Our most ambitious scene of a Gay 90's Christmas Party had fourteen moving figures! But the marvel of it all to me was how Dick arranged each figure's movement, all by the use of 2 or 3 motors, one being an old phonograph motor that he had to gear down to slow the motion.

In a paper on the new genus *Elsiella,* Dick wrote a paragraph dedicated to me, and now I'd like to respond. In the forty-five years of our marriage, his wide and deep knowledge of entomology and other biological fields, philosophy and semantics, his great teaching skill, his appreciation and constant encouragement of my career as a scientific illustrator, his willingness to help others, and ability to always see humor in the world have enriched my life more than I can ever say.

J. New York Entomol. Soc. 94(2):141–144, 1986

THE YOUNG RICHARD CHARLES FROESCHNER: EMERGENCE OF A PROFESSIONAL ENTOMOLOGIST

PAUL, THE REV. ROBERT, AND THE REV. WILLIAM FROESCHNER
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We, the three brothers of Richard Charles Froeschner, have gathered together to write an appreciation of Dick in his earlier years as a budding entomologist. From that early, deep interest in insects and natural history he has never wavered.

Born in Chicago, Illinois, March 8, 1916, Dick is the second son of Paul D. Froeschner and Helen Kaltenbach, who came to the United States from Germany as children. Our parents had little education, were poor, frugal, and steeped in a strong "work ethic." This was passed on to the next generation, and seeing the opportunities that existed in their new homeland, they insisted on high school educations for us: Paul, the eldest by seven years; Richard; Robert; and William, the youngest by five years. Paul, an avid reader of scientific subjects, became the mentor for his brothers in their developing interest: Richard in entomology; Robert in herpetology; and William in botany. The younger two of us entered the ministry as our profession but little did our parents dream that their second son would emerge a Ph.D. and a well-known entomologist.

Early in life, the four of us became interested in natural history. Each spring and summer we collected and displayed animals in a backyard "zoo." A title board tacked to the grape arbor, which shielded cages from the hot sun, bore the words "F. N. C. Zoological Gardens." "F.N.C." was based on the first letters of the ill-defined "Froeschner's Nature Club." Residents of the sundry home-made cages, bath tubs, and fenced areas were largely reptiles, though other animals appeared from time to time. A young full-grown coati-mundi, which entertained the premises for a season or two, was an expert in rooting out the termites and "water bugs" that inhabited the wooden retaining walls beneath the fences. The animal with the longest residency was a red-faced rhesus monkey, given to the Froeschners because no one else wanted the cantankerous critter. We remember with a smile the four-foot alligator that escaped from its enclosure one night, had its picture on the front page of the morning paper, and had to be reclaimed from the local police station by two sheepish brothers; the large litter of common water snakes that slipped through the cracks in their mother's enclosure and caused mild havoc in the neighborhood; and the quarrelsome rhesus, turned loose from her chain to evacuate reluctant children from the "zoo" at closing time.

Inspired by the then current and popular jungle films by Martin and Osa Johnson and "Bring 'em back alive" Frank Buck, the Froeschner Nature Club discovered its own natural paradise in a superb woodland and savannah area near Moline Creek, not too far from home. Now the area is overgrown with residences, commerce, and even a shopping center. Then it was an area rich in the flora and fauna of Missouri; treks through the humid undergrowth were often rewarded with discoveries of clearings where butterflies of every description met at moist clay watering holes.

In those years youth in the Walnut Park area of St. Louis showed such interest in animal life that the local branch library reserved several shelves for often-borrowed books on reptiles and insects. One of our associates in "the Park" was the late Richard Grossenheider. He became a well-known animal artist whose works continue to appear in publications and displays. A hardware store even "contracted" to have one of its display windows decorated for successive weeks with woodland scenes and living animals. All went well until a cottonmouth or water moccasin somehow escaped from the window. Customers who learned of the mishap were reluctant to enter the premises. Finally, when the owner discovered the venemous snake lying near the crank that he used daily to open and lock the safe, all future displays were cancelled immediately and replaced by more traditional inert hardware.

While Dick demonstrated an all-inclusive curiosity about living things, insects intrigued him the most. Paul recalls how Dick, at age 3 plus, was noticeably attracted to insects felled by coal oil lamps at home; further, how at the age of five, he was fascinated by the jerky antics of "sand bees" as they kicked grains from cracks in exterior walls of the house and stuffed and sealed immobilized insects into the "little rooms" where they had laid their eggs. At age 12 he made his first butterfly net from a broomstick, a piece of stout barrel-stave wire, and ten-cents worth of cheese cloth. Later, after we saved sufficient nickels and dimes by regularly walking the three miles home from high school, a sophisticated metal take-apart-for-travel net was ordered from a Chicago firm. It was a proud day when the contrivance arrived. Only after the net was carefully screwed together did we take turns making practice fore- and backhand thrusts through the air.

Another net was added to the "tools" when Dick discovered a discarded tennis racket at the local dump. A remarkably sturdy instrument was produced in a few hours using the frame, scissors, string, needle, and some sack cloth. The cloth was colored green with the then popular Rit dye. The finished product was called a "beating net," an appropriate name because it was designed to thrash one's way through fields of weeds, netting insects (and leaves!) from their hiding places in the dense growth. We have vivid recollections of Dick vigorously whipping weedy patches, then squatting at the end of each sweep to carefully unfold the net laid across his knees. Ever-present killing jars, carried in the twin pockets of his long-sleeved chambray shirt, darted to and from their places as specimens were harvested. The captives not desired were permitted to go their way unharmed. Neither summer heat, angry wasps, hungry mosquitoes, nor Missouri chiggers could stop his forays. Indeed, so many insects were collected in this manner that years later he was still "working" on them.

A word about those killing jars deserves mention—they, too, were homemade. An important ingredient was cyanide. One year, Paul, in an effort to get Dick "just the birthday gift he needed," approached the druggist with a request for some cyanide "eggs." The druggist hesitated a bit, saying cyanide was hardly a fitting birthday gift, but he finally agreed to order the lethal stuff because he was acquainted with the family's peculiar habits and felt reasonably comfortable with the request. Those were the years when local merchants knew their customers and there were few restrictions on dangerous substances.

Still another tool designed by Richard was dubbed a "grubber." A rusty steel bar about the length of a crowbar was heated so that one extremity became a three-inch bend. The end of the bend was hammered and filed to make a broad screwdriver-like tip. With it, fallen rotting logs could be hacked and pried open to reveal their contents, with mice often dislodged in the process. On one occasion some white-footed deer mice became part of one winter's remnant zoo in the family basement. Another time four delicate flying squirrels made a hasty exit from their nest high in a dead tree that was being prodded at the base. It is difficult now to recall how many species of ants, borers, roaches, and other creatures were gathered from such "grubbings." Unforgettable, though, was the first sight of immense sound-producing beetles and their huge grubs. Subsequent research revealed that the scientific name was *Passalus cornutus* and that the raspy sound they emitted was a primitive form of communication required in their deep, dark habitat. Dick's expanding interest in the six-legged creatures led him to secure yucca plants for the family yard to attract yucca moths. The experiment succeeded and there was excited rejoicing among us.

Another quite different collecting practice comes to mind. At dusk, in a wooded area, a mixture of stale beer and spoiled jelly was painted heavily on a line of tree trunks. At intervals during the night, with the aid of lanterns and a flashlight, the trees were inspected. Interesting assortments of insects were found feeding on the sticky, smelly substance. During one night's watch, cold winds began to blow atop a high hill overlooking Grafton, Illinois, and two shivering brothers were forced to button their collars, lower their sleeves, roll up in their light summer blankets, and crouch in a hole that looked very much like a grave dug but never used. The experience disturbed no one but the shivering boys.

Other incidents, however, led to different consequences. The landlady of Dick's student residence found a sack of rattlesnakes beneath his bed (they were to be sent to Elmhurst College for his brother Bob's student lecture on reptiles). Kindly, Mrs. Cooper confronted him with an ultimatum: "Either the snakes go, or you and the snakes go together." He quickly found a different storage space! On another occasion, our mother scolded him about keeping tarantulas caged in a flimsy ice cream carton. On yet another, this while in army basic training during a ten-minute rest break, the sergeant, after observing Richard turning over rocks and logs to study the creatures beneath, made some spicy comments questioning the recruit's sanity.

Along with the collecting, of course, came the need for "spreading" boards and storage cases. In the depression years there was no money to buy them, so wooden fruit boxes were "liberated" from grocery store trash burners and, on Dad's work bench, the slats and ends were turned into serviceable items. As an extremely resourceful person, few obstacles stood long in Dick's way.

John Henry Comstock's *An Introduction to Entomology* become Dick's handbook. A worn copy of that volume still resides on a bookshelf in the old family home.

Bob's purchase of a 1928 Model A Ford coupe, a set of inexpensive tools, tire patches, and baling wire facilitated field excursions to more distant places. When Bob announced plans to enter Elmhurst College (near Chicago), Dick thumbed his way home from the University of Missouri to make an exchange: his old worn Gladstone suitcase for his brother's old worn Ford—"Even Steven!" Subsequently, Dick's collecting trips around Missouri were limited only by the need for major repairs (most of which he could do himself) and money for gasoline. In the university years, he made friends with other young scientists. One, later to become widely known for his research into the history and ways of native American Indians, was Dr. Carl Chapman. The two frequently traveled together on field expeditions. Another friend, whose name we never knew, was doing research on intestinal parasites of skunks. Dead skunks found on the road were scooped into the car, taxied back to Columbia, and deposited in a laboratory refrigerator until the doctoral candidate could examine them. Even repugnant odors were no major deterrent. In Dick's relentless quest for insects, he frequently turned over the bodies of horses and cows left in fields to decay. Beneath them were rove beetles and other carrion eaters surrounded by a "distinctive" atmosphere. During college vacations, Dick worked a summer each in the Dutch elm disease program and on Japanese beetle research. Traps used in the latter work gathered a number of species other than the Japanese pest, which became his merely for the taking.

School teachers along the way were of great assistance to Dick. Miss Lenzen, an eighth grade teacher, encouraged his curiosity through conversation and suggested reading material. Dr. John Prather, a humble but demanding high school biology teacher, deeply impressed the Froeschners. At his urging they helped form an after-school dissection club, which provided advanced learning and invaluable hours of association with this remarkable, though little-known, zoologist. Most helpful, however, was a Miss Mary McCarty, another high school biology teacher. Recognizing Dick's potential, she acted to further promote it. She drove him to the University of Missouri, introduced him to the biologists, and personally negotiated hard-to-get grants with a depression-plagued administration, all of which allowed him to begin his career as an entomologist.

It is unfortunate that none of these people lived to see their protege honored with this issue of the *Journal of the New York Entomological Society* celebrating his seventieth birthday. It is probable that his good experiences with these helpful people gave him insight into the value of taking a personal interest in his own students. In 1958, while Associate Professor in Zoology at Montana State University, he was voted Distinguished Teacher of the Year; this honor carried a certificate and cash award. Many of his students must still look back with appreciation for the knowledge he shared and the manner in which he helped them grow.

A few sentences must be written about his wife and family. Dick's wife, Elsie Herbold Froeschner, also the child of a German immigrant family, met and married Dick while at the University of Missouri. To their marriage, Elsie brought her own extensive knowledge of the natural sciences and enviable artistic skills. Her accurate, detailed drawings have greatly increased the value of Dick's publications. Her sketches regulary appear on the couple's Christmas greetings, and her paintings have graced the walls of friends and relatives fortunate to have received them.

Elsie's consideration as a wife and mother has enriched Dick's life in ways that freed him to pursue his career with devotion seldom achieved. Two daughters, Ellen and Kay, now grown, and two grandchildren are treasured parts of their lives.

In this public recognition of his seventieth birthday, all who have assisted him or learned from him, can join his family in being proud of their association with an entomologist extraordinary, Dr. Richard Charles Froeschner.

J. New York Entomol. Soc. 94(2):145–147, 1986

A STUDENT'S REMEMBRANCE OF DICK FROESCHNER

Paul L. Eneboe
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When I first received an invitation asking me to write an appreciation of Dick Froeschner, I was more than a little overwhelmed. What could a country doctor who has spent 20 years practicing in rural Alaska have to contribute to a learned journal of entomology? My entomology has disintegrated to an ongoing war with mosquitos and treating "bug" bites, the subtleties of Hemiptera, Heteroptera, and Homoptera long since forgotten. But I have not forgotten Dick Froeschner.

As we go through life we are indeed privileged if we have one truly great teacher, a teacher who reaches inside and turns something on, or changes our lives, opens up new worlds or makes us see the old one differently. Such teachers are rare. I've been lucky. I've had many good teachers, lots of excellent ones, a few great ones, and one truly great teacher. That man was Dr. Richard Froeschner. I think often of Dick and the many things he taught me, and of his great good humor.

The first time I met Dr. Richard Froeschner was in the mid 1950's at Montana State College (it has since dubbed itself a University and raised tuition). I was an Aggie, a wiseacre major in animal husbandry, who took a course in zoology out of boredom. It was one of those glorious days as only a brilliant fall day in Montana can be. I was in my usual classroom spot, which was the back row looking out the window wishing I were anywhere but in college, and wondering whatever I was doing in a course that looked like it might take some work and thinking seriously of dropping it. Dick Froeschner entered the room—bounced is more the word—with a disarray of yellowed papers under his arm and wearing a sport shirt and open-toed sandles (a social outrage in Montana in the 1950's). The disarray of papers spread across the podium. Dick Froeschner looked at the class, grinned, and commenced what was for me one of the most significant hours of my life. For the first time I heard someone who really made sense. He talked about life, about science, and about what he hoped to teach us that year. I was never really sure whether he talked or just enthused. But the next day I moved down to the front row and stayed there. During that year Dick Froeschner covered zoology from bottom to top in one of the hardest, most fun, most challenging courses I've ever taken. He taught much more than zoology—he taught about life. Throughout the course a recurring theme was a great tree of life which, unlike the dead trees so commonly found in biology books, Dick made into a living thing that changed and grew, full of mystery and surprises. Dick taught us also about science, scientific inquiry, experimentation, and truth. His lectures were animated and fun, full of examples that caught the imagination. His blackboard danced with small creatures to illustrate some point or another.

I wasn't the only one who was spellbound. After every lecture a goodly part of the class would spill into Dick's office next door where the students encountered skeletons, rattlesnakes in cages, piles of books, and an even bigger disarray of papers. Dick would patiently answer questions, stimulate arguments, and challenge us to think and reason. No question was too silly or sophomoric to deserve a considered answer, which often would illustrate a fundamental point in biology. Dick Froeschner had a loyal and consistent following of students and was one of the most popular and most respected teachers on campus.

The next year I followed zoology with Dr. Froeschner's course in entomology, where he rose to new heights because that's where his love was. That year I learned from Dick so much more than the usual mandatory review of the insect world and its cousins. Again he taught of the wonder of life, how things changed, and how they are related to each other, and the excitement of looking for and identifying new things. That year Dick also taught us about work and challenges. He had acquired several books and papers written in Russian, a language unfamiliar to him. Midway through the year he bought several Russian dictionaries, opened the largest tome of entomology I'd ever seen and with dictionary started at the first page. He learned enough Russian to grasp the meaning of articles dealing with Hemiptera, and had fun doing it. He tried to teach some of us Russian (probably one of his few failures). But what he did teach us was that no task was too impossible or difficult if it really needed doing.

I was fortunate to become Dick's lab assistant in general zoology. Working with him was a chance to see his disciplined and ordered approach to teaching and to appreciate his good humor. One of the events of the year was known among students as Froeschner's Bug Feast, in which Dick supplied delicacies from the insect world which were consumed with varying degrees of enthusiasm.

No one ever explained quite how it happened, but during those years the zoology lab became the gathering place for an ongoing debate on just about anything debatable. Somehow physics majors, chemistry and biology graduate students, and various lab assistants would drift into the zoology lab. It was nothing formal or organized, it was one of those things that happen. The arguments never really began or ended, but just continued. Occasionally they would drift over to the student union building, but almost always they stayed in the lab room. Dick Froeschner would be puttering around with lab specimens, not quite involved in the discussion, which generally had to do with such things as infinity, dimensions, the definitions of life, and other subjects that were terribly important and urgent. The arguments, always animated, were occasionally heated. Dick would be silent through most of them. At the oddest moments he would ask a question or make a comment over his shoulder, which in a few words would center the entire discussion. He would in a word illustrate some fundamental point of science or some obvious truth we were all missing. It was with a few words at just the right time that Dick Froeschner taught us what scientific inquiry really means. He taught us about rational thought and relevance and truth. He taught us that scientific truth was hypothesis and theorem and proof and fact, and that theorems change, but truths and integrity do not. He challenged us to reason through a problem, to see the subtleties of an issue, and to look through the complexities to the simple answers.

Many times over the years I have thought of those days sitting on the edge of a lab table waiting to make a point or covering the blackboard with chalk to demonstrate one. And Dick with a quiet smile keeping things going, not infrequently by changing sides in the argument midway through and leaving us all sputtering. Dick never lost patience and would sit through the most silly arguments, sometimes until late in the evening, always guiding and teaching.

There was another place that Dick Froeschner could be found besides the classroom and the teaching laboratory. High up under the rafters, the top floor of Lewis Hall housed the entomology collection—quiet and dusty, trays and trays of mounted insects carefully classified and arranged, a large working table with microscope, and the usual disarray of papers, somehow more neatly arranged. Scattered among them were many of Elsie's wonderful drawings, papers in progress, notes and letters from colleagues, and dozens of specimens waiting to be classified, along with books in a dozen languages. That was not the domain of Dick Froeschner, teacher and friend, but that of Dr. Richard Froeschner, entomologist and researcher. It was here that Dick so often said he recharged his batteries, for as much as he loved teaching, his life was research. Dick said many times that research was the fuel that kept him going.

No man could continue to carry the load of full-time teaching and full-time research that Dick did. He put too much energy into both, and he had to make a choice. He did, and he made the only choice that Dick Froeschner would ever make—he chose research. My senior year of college Dick Froeschner left Montana State for Washington, D.C. and a career in research. Lewis Hall and the Biology Department seemed empty and quiet when Dick left. The discussions in the zoology lab dwindled and disappeared, and some of the zest and energy in the department left with him. There were other good men there, wonderful teachers and good friends. But somehow when Dick Froeschner left the sparkle that all of us felt, students and teachers both, was gone.

Shortly before he left, Dick invited me to his house for dinner with him and Elsie. No mention of Dick Froeschner would be complete without a word about Elsie, her great good cheer, tremendous interest in life, and wondrous drawings and illustrations. I remember that evening as we talked long into the night. By that time I had transferred from the agricultural college to biology and was seriously considering entering medical school. Dick talked at great length (dare I use the word harangue) about the joys of research and pure science as opposed to what he considered the witchcraft of medical science.

I'm afraid I was a great disappointment to Dick. I fell from the path of truth and righteousness and entered medical school. But it was Dick Froeschner's teachings that carried me through. Since I entered practice, I cannot count the number of times when faced with a difficult or seemingly unsolvable problem I've thought back to Dick Froeschner and the way he approached the unknown and was able to solve or work through a difficult situation. It's been far too many years since I've seen Dick Froeschner, something I hope to rectify in the near future. But I shall always be grateful for what he did. He taught me to think.

J. New York Entomol. Soc. 94(2):148–153, 1986

A NEW, EXTREMELY BRACHYPTEROUS SPECIES OF *ONCYLOCOTIS* FROM ZAIRE (HETEROPTERA: ENICOCEPHALIDAE)

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Abstract.—*Oncylocotis froeschneri,* new species, based on an extremely brachypterous male from Zaire is described and illustrated.

Oncylocotis Stål, 1855 (=*Dicephalus* Kirby, 1891; *Sphigmocephalus* Enderlein, 1904; *Didymocephalus* Jeannel, 1942) is the largest genus of Enicocephalinae with numerous, mostly undescribed, species occurring in the Afrotropical, Madagascan, and Oriental regions (as well as along the southern fringe of the Palearctic), New Guinea, Pacific islands, Australia, and Tasmania. The generic placement of a few species now included in this genus from Neotropical region will be settled in a monograph on American enicocephalids under preparation by P. Wygodzinsky and K. Schmidt, American Museum of Natural History, New York.

Most species of *Oncylocotis* are macropterous to submacropterous; some exhibit continuous or discontinuous pterygopolymorphism, and range from macropterous to strongly brachypterous; some are known to occur in only one stage of this continuum. Forewings of females tend to be slightly shorter, but the forewing reduction is essentially not sex-linked. However, forewing reduction is linked with many phenotypic changes in the general facies of individuals or taxa, including the following: reduced venation (some transverse veins may be missing); shorter, narrower, and posteriorly less excised posterior lobe of pronotum, and less developed sculpturation of the middle lobe; more robust head; thicker and shorter antennae; smaller the eyes and ocelli, and more transverse posterior lobe of the head; and thicker and shorter legs. In *Oncylocotis neotenicus,* the one truly micropterous species (forewings reduced to widely separated vestiges without any traces of venation and fractures, not extending beyond the metathorax, hindwings absent), known from Sumatra, even the shape of the male abdomen and genitalia is affected (Štys, 1982). This picture is further complicated by the gynaecoid characters of females: they tend to be shifted—even if the size of forewings is not affected—toward that part of the above-mentioned spectrum of character states associated with forewing reduction.

All of this complicates the taxonomy of the genus, which is in a rather unsatisfactory state. In addition to the now outdated worldwide survey of species by Jeannel (1942), there exist only the surveys of Afrotropical and Madagascan species by Villiers (1969) and Micronesian species by Usinger and Wygodzinsky (1960). However, Villiers's approach to the diagnosis of species was rather typological, and hardly any attention was paid to modifications of characters by pterygopolymorphism and sexual dimorphism.

The forewings of even the most brachypterous phena (termed "micropterous" by

Jeannel, 1942, and Villiers, 1969) of described Afrotropical species are rather long, reaching at least onto the 4th abdominal tergum, slightly overlapping and retaining distinct though reduced venation; the hindwings are shorter but well developed. However, when examining the collections of Musée Royal d'Afrique Central in Tervuren in 1966 and 1968, I noticed that the material of *Oncylocotis* identified by A. Villiers as "unidentifiable larvae" also included some extremely brachypterous adult specimens with shorter, scalelike, non-overlapping forewings, and indistinct venation. Through the kind assistance of Dr. H. M. André (Tervuren) I have been able to examine this material in detail. Some of these extremely brachypterous specimens represent new species or belong to taxa previously known in the macropterous form only; they will be dealt with in another paper. In the present one I describe one of the brachypterous forms, which undoubtedly belongs to a yet unknown species.

Dedication. I have the honor to dedicate this paper and to ascribe the name of the new species to my scientific friend Dr. Richard C. Froeschner, hemipterist of the National Museum of Natural History, Washington, D.C., on the occasion of his 70th birthday and in acknowledgment of his great contribution to hemipterology and his frequent help to me.

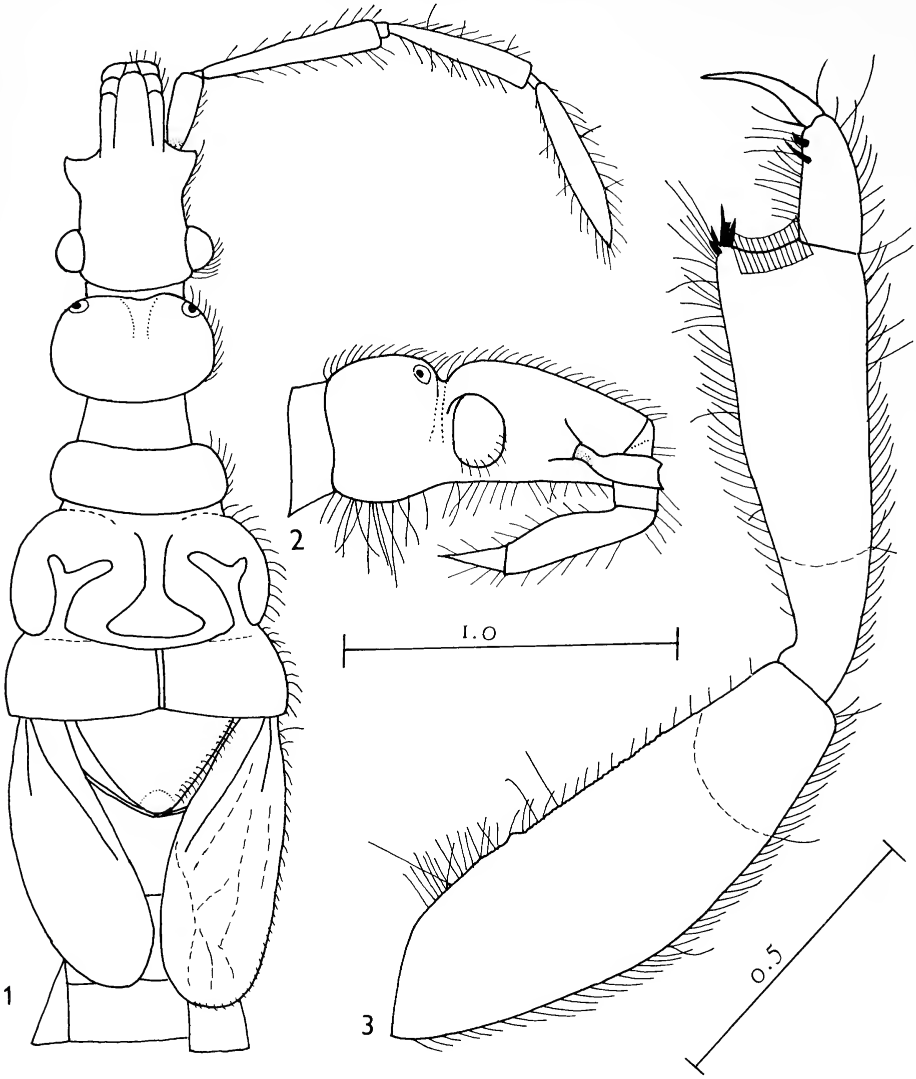
Oncylocotis froeschneri, new species

Figs. 1–5

Description. Extremely brachypterous male. General facies. Small, slender, gracile, bicolorous (head, forewings, legs), narrow species with rather short and thick antennae, moderately long legs, and mostly short, but not uniform pilosity.

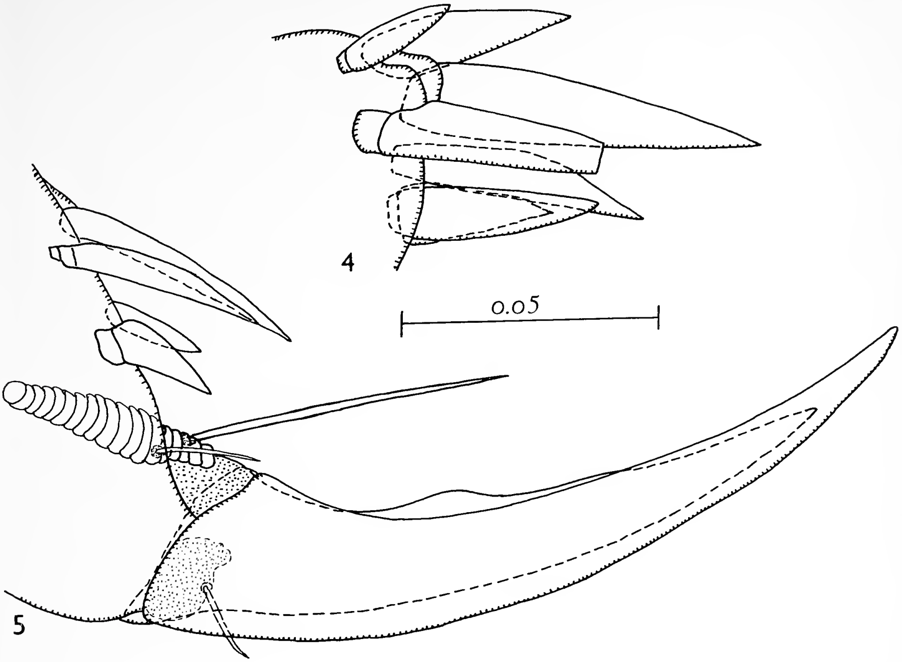
Measurements (all in mm; L = length, W = width). Total length 3.95. Head, anterior lobe: L 0.61, anteocular W 0.26, distance eye–apex of antenniferous tubercle 0.20, distance eye–base of antenniferous tubercle 0.09, L of eye 0.16, interocular W (min.) 0.28, transocular W (max.) 0.46; posterior lobe, L 0.34, W 0.46. Lengths of antennal segments (II–IV inclusive proximal intercalary segments): I 0.15, II 0.51, III 0.50, IV 0.54. Labium, segment III, L (ventral) 0.45, height 0.12; IV L 0.17. Pronotum: collum, med. L 0.22, max. W 0.45; middle lobe, med. L 0.37, max. W 0.74; posterior lobe, med. L 0.19, max. W 0.81. Mesoscutellum, L 0.31. Forewing, L 0.84, max. W 0.31. Fore leg: femur, L 0.87, max. W 0.28; tibia, L 0.74, max. W 0.25; tarsus, L 0.20, max. W 0.11. Middle tibia, L 0.71. Hind tibia, L 1.05. distance apex of head–apex of mesoscutellum 2.08.

Coloration. Bicolorous, rather dull, ground color of body dark brown to blackish brown. Posterior lobe of head contrastingly dull orange, collum and posterior lobe of pronotum lighter (brown with some orange shades) than middle lobe (blackish brown), frenae of mesoscutellum light brown. Antennae brown, segment 4 orange-brown. Proximal ¼ of forewing noncontrastingly but distinctly paler (dark stramineous) than distal part (brownish). Ground color of fore leg dark brown to orange-brown (apex of tibia, tarsus), "knee" (distal ¼ of femur on posterior face, ⅕ on anterior face, proximal ¼ of tibia) contrastingly lighter (dull stramineous). Coloration of middle and hind legs similar, but ground color lighter, pale areas involving also coxae and trochanters as well as extreme bases of femora; pale "knees" occupying the distal ¼ of middle femora and distal $^1/_6$ of hind femora, but hardly recognizable on very pale, stramineous tibiae (also middle and hind tarsi stramineous).



Figs. 1–3. *Oncylocotis froeschneri,* ♂ holotype. 1. Head, thorax, wings and antennae in dorsal view. 2. Head and labium; lateral view. 3. Right fore leg, anterior view; dashed lines indicate the extent of pale "knee." Only marginal hairs illustrated. 1 and 2 drawn to the same scale.

Pilosity of dorsal and lateral sides of head, and of thorax, legs, and wings moderately dense, mostly erect or diagonal, uniformly short, inconspicuous, only that of the posterior lobe of head slightly longer, curved, and adpressed. Hairs on the venter of head longer and semierect below eyes, longer and curved on lateroventral sides of posterior lobe; the ventral side of the latter with a sparse group of long, soft, erect hairs, the longest about 0.5 times as long as posterior lobe is high.



Figs. 4, 5. *Oncylocotis froeschneri,* ♂ holotype. 4. Apicitibial armature of right foreleg, anterior view. 5. Tarsal armature and pretarsus of right foreleg, anterior view. Drawn from cleared slide preparation; setae omitted. Same scale for both illustrations.

Cuticle matt to slightly shiny, only impressions of middle lobe of pronotum markedly polished. Setigerous tubercles absent.

Head as illustrated (Figs. 1, 2). Constriction situated immediately behind eyes. Ratio length of eye: (distance eye–base of antenniferous tubercle) about 0.6. Eyes small, only laterally situated, sparsely and only ventrally pilose, ocular index 3.0; facets normally developed, packed closely together. Posterior lobe transverse, 1.45 times as wide as long, widest in the middle, lateral sides regularly rounded; median marked by proximal, shallow, rather broad concavity, no linear impression present. Ocelli present, small, facing laterad, situated on small, polished, hardly elevated, red pigmented areas.

Antenna (Fig. 1) 1.58 times as long as head without neck, rather thick, segments 2–4 subequal in length, 2 and 3 proximally narrow, markedly thickened distally, 4 fusiform. Pilosity of antennae semierect, sparse, rather short, that of segment 4 shorter than segment diameter.

Labium (Fig. 2) rather thick, 3rd segment 3.6 times as long as high and 0.9 times as long as 2nd antennal segment, its dorsal outline markedly convex (lateral view).

Pronotum (Fig. 1) as illustrated; collum simple, without lateral tubercles, median indistinctly concave; both medial and lateral impressions of middle lobe complete, well developed, the anterolateral arms of Y-shaped impressions abbreviated; posterior lobe strongly reduced, posteromedially shallowly subangularly excised, otherwise posterior margin nearly straight, median with a low, percurrent linear keel; proportions of median lengths of collum:middle lobe:posterior lobe as 7:12:6, of their maximum widths as 7:12:13. Mesoscutellum roundly triangular, its frenae retained.

Forewings elongate oval, 2.7 times as long as wide, the left one reaching the posterior margin of abdominal tergum 2, the right one the middle of tergum 3. Forewings widest in ½ of their length, not overlapping, hardly mutually contacting. Vestiges of venation present, but indistinct and not interpretable; claval fracture retained as a long furrow running up to the level of maximum width of wing, medial furrow proximally distinct. Hindwings reduced to short scales (articulating?) hardly reaching ½ the length of lateral margin of metapleuron.

Fore legs (Fig. 3) moderately thick, femur 3.15 times as long as wide, tibia 3.00 times as long as wide, tarsus 1.87 times as long as wide (based on maximum values from cleared, not deformed slide preparation). Femur without setigerous tubercles, its ventral face covered with numerous, sharply delimited, minute semispherical microtrichia (about as wide as alveoles of setae); hence ventral profile of femur mini-crenulate. Shape and pilosity of leg as illustrated. Apicitibial projection short, with 7 spines[1] (Fig. 4), one of them truncate (possibly a natural state, observed also in other *Oncylocotis* species). Apical tibial comb of 32 setae. Tarsal armature and pretarsus as illustrated (Fig. 5). Anterior (inner) claw only slightly longer than posterior (outer) claw, but anterior (sic!) parempodial seta only about 0.25 times as long as the posterior one. Dorsal arolium with a distinct, short aroliar seta (overlooked in previous studies of the genus).

Abdomen without particulars, segment 8 normally developed, flat, not affected by neoteny (*cf.* Štys, 1982). Pygophore small, but protruding and terminating the abdomen, truncately subspherical. Genitalia (hardly diagnostic for species of this genus) not examined.

Etymology. The specific name is derived from the name of R. C. Froeschner.

Holotype. ♂, ZAIRE, Kivu, Uvira, 3.24°S, 29.05°E, i. 1958, N. Leleup; in vestiges of sclerophyllous forest. Right fore leg detached and preserved in a pinned glycerine microvial. Deposited in Musée Royal d'Afrique Centrale, Tervuren.

Discussion. Oncylocotis froeschneri belongs to an aggregate of species characterized by bicolorous legs and forewings and will fit couplet 10 in Villier's (1969) key to Afrotropical species. This couplet contains *O. mirei* (Villiers, 1960) known from the Sudan, Tanzania, and Cameroon, and *O. angolensis* (Villiers, 1959) from Angola and P. R. Congo. Both of these species are macropterous, slightly larger (length 5 mm), and their antennae much thinner; the posterior lobe of the head in *O. angolensis* is more transverse than in *O. froeschneri.* The next most similar (and probably most closely related) taxon is *Oncylocotis basalis curculio* (Karsch, 1893) (*sensu* Štys, 1969; =*Oncylocotis curculio auct.*, e.g. Villiers, 1969), an Afrotropical subspecies of a widely distributed African, Arabian, and Oriental, continuously pterygopolymorphic species. *Oncylocotis froeschneri* differs from *O. basalis curculio* by its much smaller size (3.95

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[1] Outlines of some spines almost overlap when examined in slide preparations. This may indicate that the lower number of spines given in detailed descriptions and illustrations of this character in other *Oncylocotis* species (Štys, 1982; Usinger and Wygodzinsky, 1960) is erroneous. The presence of 7 spines seems to be a plesiomorphic and modal character in the family.

× 6–8 mm), much sparser and shorter pubescence of the body (especially on the dorsal and lateral sides of the posterior cephalic lobe), less pilose antennae and legs, distally more widening antennal segments 2 and 3, more extensive pale areas of "knees," and a generally duller and less contrasting coloration. The reduced forewings of *O. froeschneri* differ from those of the most brachypterous morph of *O. basalis curculio* by extending at most to the middle of abdominal tergum 3 instead of reaching the middle of tergum 4, by hardly recognizable rather than distinct veins, by uniformly short rather than alternately short and long semierect pilosity, and by only a small rather than striking contrast between their proximal pale and distal dark parts. No other taxon of this aggregate of Afrotropical species is known to exhibit pterygopolymorphism; most species are macropterous, and only *O. micropterus* Villiers, 1969, from the Ivory Coast is strongly brachypterous, but differs from *O. froeschneri* by much longer forewings (reaching half the length of abdomen), uniformly short pubescence of the head and pronotum, and an extremely small size (2.75 mm).

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J. New York Entomol. Soc. 94(2):154–162, 1986

LIFE HISTORY AND LABORATORY REARING OF *BELOSTOMA LUTARIUM* (HETEROPTERA: BELOSTOMATIDAE) WITH DESCRIPTIONS OF IMMATURE STAGES

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Abstract.—The life history of *Belostoma lutarium* was studied in southern Illinois, and the immature stages are described. The bug also was reared from egg to adult in the laboratory. This apparently bivoltine species overwintered as adults in leaf litter and detritus in very shallow water along the shoreline and became active in early March. Eggs were found between the 3rd week of April and early August and were laid on the backs of males. First instars appeared in early May followed by marked overlapping of the subsequent instars. Active adults were last observed in November. This species was reared on *Chaoborus americanus* larvae under a 16L: 8D photoperiod at 26.7 ± 1.5°C. The incubation period averaged 9.9 days. Durations of the 5 subsequent stadia averaged 6.3, 6.4, 10.7, 12.9, and 13.7 days, respectively.

The giant water bug *Belostoma lutarium* (Stål) is primarily a species of the southeastern United States; it has been collected from Massachusetts south to Florida, and west to Michigan, Illinois, Kansas, Oklahoma, and Texas (Lauck, 1964), but apparently has not been found in New York or Pennsylvania. *B. flumineum* Say, which occurs in the southern half of Canada, throughout the continental U.S., and in northern Mexico, becomes rather scarce where its range overlaps that of *B. lutarium* (Lauck, 1964). In Illinois *B. flumineum* occurs primarily in the northern ⅔ of the state and *B. lutarium* in the southern ⅓, with little overlap in their ranges (Lauck, 1959).

Little is known about the life history of *B. lutarium.* It has been taken from pools and ponds containing cattails, along grass borders and among stems of *Polygonum,* in shallow stock ponds filled with submerged and emergent vegetation, and from ponds and swamps with abundant growth of emergent grasses (Bobb, 1974; Lauck, 1959; Wilson, 1958). Adults have been collected in Mississippi from March to November, egg-carrying males as early as March, and nymphs from June to November (Wilson, 1958). Nymphs have been collected in Illinois as early as late May (Lauck, 1959).

For the past 3 years (1983–1985), we have studied the life history of a population of *B. lutarium* occurring in the La Rue-Pine Hills Ecological Area. This area, located ca. 18 miles northeast of Cape Girardeau, Missouri, in the northwest corner of Union County, Illinois, is part of the Shawnee National Forest. It encompasses only about 3 square miles, but contains both dry forests and hill prairies atop limestone bluffs, and moist forests at the base of these bluffs that surround La Rue Swamp and Winters

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Pond. These aquatic habitats are continuous, and it is here that our study was conducted. Much of the study area is blanketed with duckweeds (i.e., *Lemna, Spirodela, Wolffia,* and *Wolffiella*) along the shoreline.

This paper presents information on the life history and laboratory rearing of *B. lutarium* and includes descriptions of the immature stages.

We are pleased to dedicate this paper to Dr. R. C. Froeschner for his many contributions to the study of the Hemiptera and for his constantly warm and friendly personality and a continuing willingness to help others with their own research efforts. Thanks, Dick!

MATERIALS AND METHODS

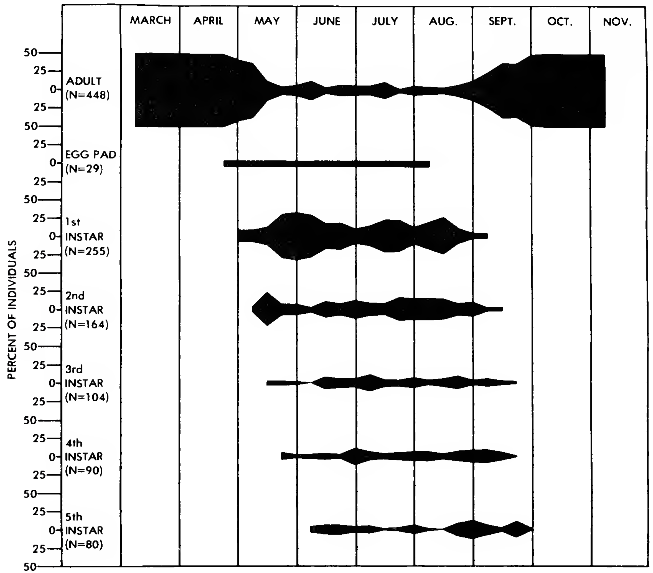
Life history. The study began in March 1983 before the bugs had emerged from overwintering sites. Samples were taken with an aquatic net at approximately weekly intervals at 6 sites along the edge of the study area into November after all nymphs had disappeared and adult activity had ceased. Sampling during the following 2 years was conducted similarly, although it ended in mid-September in 1985 when occasional nymphs (3rd–5th instars) could still be collected. All samples (minus some captured egg-carrying males that were released) were preserved in 75% ethanol and examined in the laboratory to accurately determine the developmental stages present in each sample. Occasional collections also were made during the winter months to determine ovewintering stage(s) and sites. Data gathered during the 3 years of study were combined to gain a better understanding of the annual life cycle.

Laboratory rearing. Approximately 20 adults were collected during late March and early April 1985 and returned to the laboratory. From these individuals, 7 pairs of males and females were selected and placed in 2 aquaria (4♂♂ and 4♀♀; 3♂♂ and 3♀♀). Each aquarium (ca. 30 × 20.5 × 15 cm) was covered on the bottom with aquarium gravel and filled with ca. 7 cm of dechlorinated water. Adults were maintained on amphipods, *Gammarus minus pinicollis* Cole.

Egg-carrying males were removed from the aquaria and placed in finger bowls (ca. 11 cm diam, 4 cm depth) filled with 3 cm of distilled water. All egg pads were eventually separated from the males, either by the males themselves or by us after the males prematurely died, and placed in petri dishes. Each dish (ca. 9 cm diam, 2 cm depth) was covered on the bottom with filter paper and the eggs kept moist by keeping the filter paper saturated with distilled water. Upon hatching, the 1st instars were also placed in petri dishes. Each dish was again covered on the bottom with filter paper but ca. 0.5 cm of distilled water was added, sufficient to just cover the bugs. Later instars were also provided sufficient water to just keep them submerged. About 10 1st instars were placed in each petri dish but were further separated as they developed through subsequent instars. Two *Chaoborus americanus* (Johannsen) larvae were provided daily as food per nymph, and the amount was increased by 2 for each subsequent instar. Dishes were checked daily for exuviae and any prey carcasses removed. Water and paper were changed every 3–4 days.

The aquaria, finger bowls, and petri dishes were kept in incubators maintained at ca. 26.7 ± 1.5°C and a 16L:8D photoperiod (ca. 260 ft-c).

Descriptions of immature stages. Eggs and 1st–5th instars were selected from field samples that had been preserved in 75% ethanol. The description of each stage is



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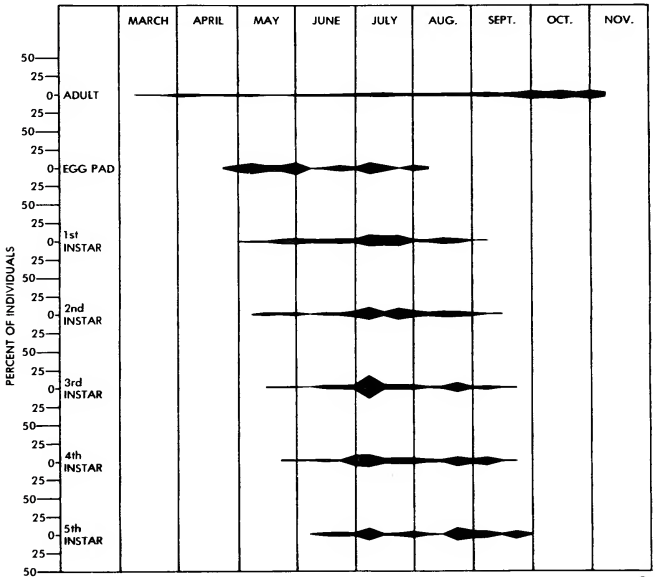

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Figs. 1, 2. 1. Percent of individuals in each stage per sample during 1983–1985 combined seasons in Union Co., Illinois. Egg pads were not included in calculations. 2. Percent in each sample of total individuals of same stage during 1983–1985 combined seasons in Union Co., Illinois.

Table 1. Duration (in days) of each immature stage of *B. lutarium* under controlled laboratory conditions.

Stage	Number completing stadium	Range	$\bar{x}$ ± SE	Cumulative mean age
Egg	182	9–11	9.9 ± 0.5	9.9
Nymph				
1st instar	148	5–12	6.3 ± 0.1	16.2
2nd instar	107	4–24	6.4 ± 0.3	22.6
3rd instar	96	4–27	10.7 ± 0.5	33.3
4th instar	95	7–24	12.9 ± 0.4	46.2
5th instar	95	10–20	13.7 ± 0.2	59.9

based on 10 individuals. Drawings were made with the aid of a camera lucida; measurements, with an ocular micrometer. Dimensions are expressed in mm as $\bar{x}$ ± SE.

RESULTS AND DISCUSSION

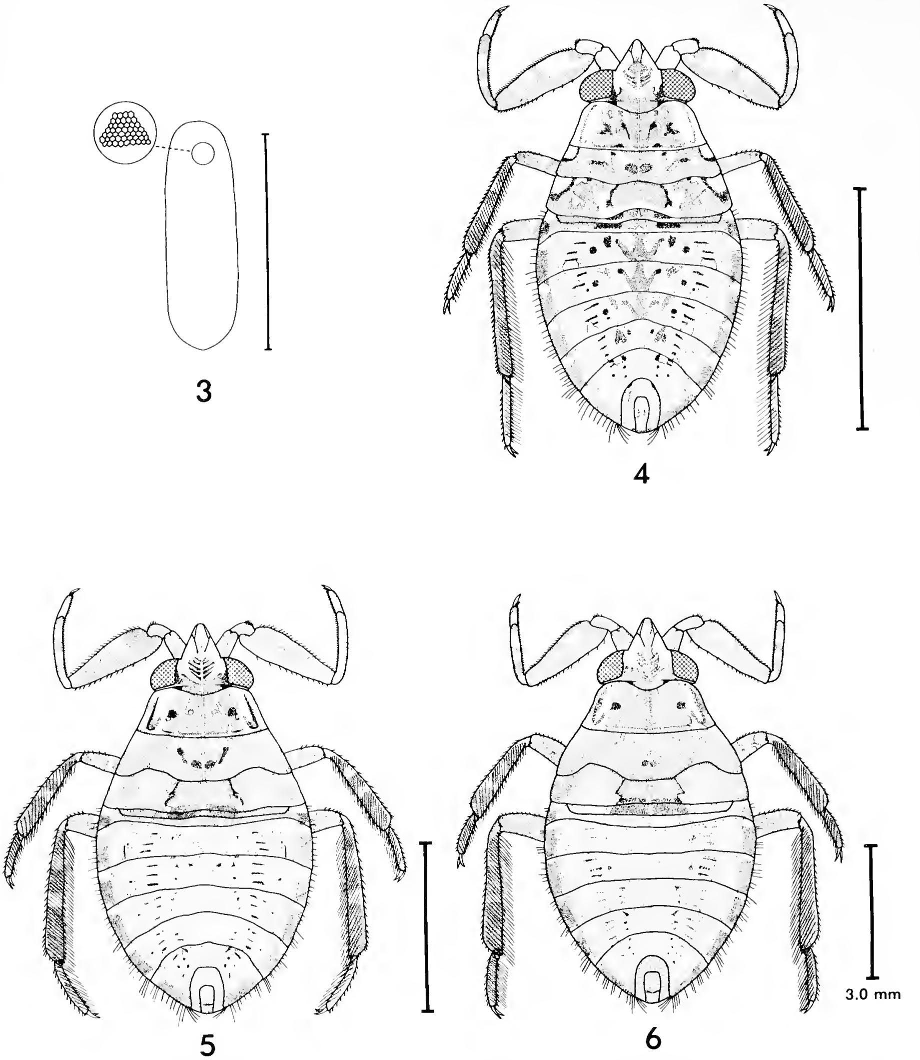
Life history. This species overwintered as adults in leaf litter and detritus in very shallow water along the shoreline, and became active in early March (Figs. 1, 2). Twenty-nine egg-carrying males were found from the 3rd week of April to early August but were most common during May (13 pads) and July (8 pads). Eggs were carried on the backs by being glued to the hemelytra. Pad size ranged from 36 to 180 ($\bar{x}$ ± SE = 116.3 ± 7.9, N = 19), which is somewhat misleading since our laboratory results showed that a pad can consist of eggs laid on successive days.

The 1st instars were found from early May to early September, 2nd instars from early May to mid-September, 3rd instars from mid-May to the 3rd week of September, 4th instars from the 3rd week of May to the 3rd week of September, and 5th instars from early June to late September (Figs. 1, 2).

Overwintered adults were most abundant during late March to May and died off soon thereafter. New adults began to appear in late June and early July as evidenced by the rise in their numbers following the 1st appearance of 5th instars. This small increase in adult numbers was followed by a much larger increase in the fall. In fact, of the 448 adults collected, 85% were collected after late June. No active adults were found after November.

This species is apparently bivoltine. Our conclusion, in part, is based on the fluctuations in numbers of the various stages during the season. Although there was marked overlapping of the various stages and, thus, any particular sample could have any combination of individuals (Fig. 1), weekly plotting of data for each stage showed 2 peaks of abundance for the eggs and 3rd–5th instars, and 3 for the adults (i.e., overwintered, summer, and fall adults); peaks for the 1st and 2nd instars were less obvious (Fig. 2).

Laboratory rearing. As in the field, eggs were laid on the backs of males. The incubation period averaged 9.9 days (Table 1). Eggs were yellowish brown at oviposition but darkened during maturation.



Figs. 3–6. Immature stages of *B. lutarium*. 3. Egg. 4. First instar. 5. Second instar. 6. Third instar.

The 1st instar emerged through a semicircular opening in the cephalic end of the egg. It was yellowish white at this time but soon darkened to its normal color. It fed on *C. americanus* larvae within 1 day.

The 1st, 2nd, 3rd, 4th, and 5th stadia averaged 6.3, 6.4, 10.7, 12.9, and 13.7 days, respectively. The total developmental period averaged 59.9 days.

Newly emerged F_1 adults placed in 2 aquaria (4♂♂, 6♀♀; 5♂♂, 7♀♀) prepared similarly to those of their parents and maintained under the same conditions matured (i.e., produced fertile eggs) as early as 21 days ($\bar{x} = 33$, range = 21–45, N = 5). This short

Table 2. Measurements (mm)[a] of *B. lutarium* instars.

	Nymph				
	1st instar	2nd instar	3rd instar	4th instar	5th instar
Body length	4.90 ± 0.03	6.88 ± 0.05	8.56 ± 0.11	13.72 ± 0.13	18.52 ± 0.30
Body width[b]	2.55 ± 0.03	3.72 ± 0.03	4.81 ± 0.05	7.48 ± 0.05	10.25 ± 0.14
Width at eyes	1.46 ± 0.01	1.98 ± 0.01	2.60 ± 0.02	3.43 ± 0.02	4.39 ± 0.04
Synthlipsis	0.67 ± 0.01	0.85 ± 0.01	1.09 ± 0.02	1.47 ± 0.01	1.90 ± 0.02
Head length[c]	0.97 ± 0.03	1.32 ± 0.01	1.61 ± 0.03	2.27 ± 0.05	2.84 ± 0.07
Pronotal length[c]	0.47 ± 0.01	0.73 ± 0.01	1.15 ± 0.04	1.64 ± 0.01	2.35 ± 0.04
Mesonotal length[c]	0.40 ± 0.02	0.74 ± 0.01	1.16 ± 0.04	1.94 ± 0.03	3.02 ± 0.05
Metanotal length[c]	0.31 ± 0.01	0.46 ± 0.01	0.62 ± 0.01	0.82 ± 0.01	0.91 ± 0.02
Leg lengths:					
Profemur	1.39 ± 0.01	1.83 ± 0.01	2.56 ± 0.02	3.45 ± 0.02	4.52 ± 0.05
Protibia	0.88 ± 0.02	1.18 ± 0.01	1.70 ± 0.01	2.30 ± 0.02	3.02 ± 0.04
Protarsus	0.37 ± 0.01	0.45 ± 0.01	0.61 ± 0.01	0.75 ± 0.01	0.95 ± 0.01
Mesofemur	1.58 ± 0.02	2.14 ± 0.01	2.86 ± 0.02	3.96 ± 0.03	5.33 ± 0.07
Mesotibia	1.40 ± 0.02	1.86 ± 0.01	2.48 ± 0.03	3.44 ± 0.02	4.62 ± 0.06
Mesotarsus	0.58 ± 0.01	0.74 ± 0.01	1.01 ± 0.02	1.38 ± 0.02	1.84 ± 0.03
Metafemur	1.85 ± 0.02	2.56 ± 0.02	3.46 ± 0.03	4.86 ± 0.05	6.56 ± 0.09
Metatibia	1.84 ± 0.02	2.53 ± 0.02	3.38 ± 0.03	4.62 ± 0.02	6.27 ± 0.08
Metatarsus	0.78 ± 0.01	1.02 ± 0.01	1.43 ± 0.03	1.95 ± 0.01	2.68 ± 0.06

[a] $\bar{x}$ ± SE.
[b] Measured across 3rd abdominal segment.
[c] Measured along midline.

prematuration period further supports our conclusion that this species is bivoltine in southern Illinois.

DESCRIPTIONS OF IMMATURE STAGES

Egg (Fig. 3). Length, 3.18 ± 0.04, width, 1.09 ± 0.01. Eggs laid in clusters (pads), affixed to backs of males by gluing to hemelytra; each egg elongate, yellowish brown at oviposition but darkening during maturation; chorion with primarily irregular hexagonal pattern.

Nymphal instars

The 1st instar is described in detail, but only major changes that have occurred from previous instars are described for subsequent instars. Length is measured from tip of tylus to tip of abdomen, width across the 3rd abdominal segment. Additional measurements are given in Table 2.

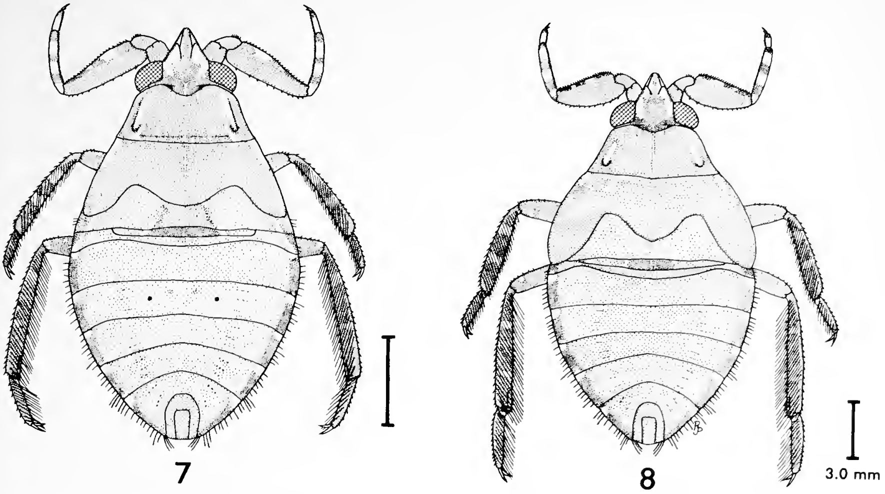
1st instar (Fig. 4). Length, 4.90 ± 0.03; width, 2.55 ± 0.03. Body broadly oval, greatest width at 3rd abdominal segment, dorsoventrally flattened; yellowish with light to dark brown maculations.

Head broadly triangular, porrect, anterolateral margins straight. Head yellowish dorsally with brown stripe along anterolateral margin between eye and apex of tylus; brown chevron-shaped mark on disc, and brown U-shaped mark along posterior margin; thin yellow line originating from inner margin of each eye anteriorly, both lines continuing posteriorly along anterior margin of U-shaped mark, meeting medially, and giving rise to short yellow line continuous with middorsal yellow line of thorax and anterior part of abdomen. Tylus elevated above and exceeding juga, apically reaching between bucculae, tylus and bucculae collectively forming a tubular socket holding modified base of labium. Eyes black dorsally, red ventrally; synthlipsis near anterior margin of eye ca. 1.8 × width of eye. Head yellowish ventrally with brown stripe either side of middle and continuous from base of beak to back of head. Antennae brownish, arising near anteroventral margin of eye; knoblike, directed anteriorly, 3-segmented, segments 1 and 2 subequal, each ca. ⅙ length of 3. Beak yellowish; 3-segmented, extending to procoxae; segment 1 subequal to 3, and ca. ½ length of 2.

Thoracic nota yellowish with brown maculations. Pronotum trapezoidal, moderately convex, anterior margin arcuate medially, posterior margin nearly straight. Mesonotum narrower, ca. 0.9 × length of pronotum along midline, with semicircular depression anteromedially; anterior margin nearly straight, posterior margin arcuate medially and sinuate laterally; wing pads weakly developed laterally. Metanotum narrowest of thoracic nota along midline, convex medially, posterior margin arcuate medially; ratio of mesonotal wing pad to metanotum along lateral edge ca. 1:1. Pro- and mesopleura brown with yellow lateral margin and medial stripe. Metapleuron brown laterally, white medially, prolonged posteriorly and partially encircling metacoxa, pleuron heavily fringed with long hairs. Prosternum brown medially, yellow posterolaterally, with small yellow notch posteromedially. Mesosternum whitish with broad, brown bar medially extending from posterior margin to near anterior margin. Metasternum whitish, triangular, with brown spot in each anterolateral corner.

Prothoracic legs raptorial. Procoxa white or white with irregular brown stripe on anteromedial surface; two brown, short, blunt projections present at base; coxa ca. ½ length of femur. Protrochanter white; subglobular, with ventral patch of setae at apex; trochanter ca. ¼ length of femur. Profemur yellow with brown maculations; thickened proximally, narrowed distally, ventral surface nearly flat but with slight median groove basally, segment bordered by row of short spines on either side. Protibia and tarsus yellow, annulated with brown; together equal to length of femur; ventral surface of each segment nearly flat but with slight median groove, segments bordered by row of short spines on either side, these rows fitting within those of femur when segments are apposed; tarsus 1-segmented, the 2 claws of unequal length.

Meso- and metacoxae and trochanters similar to those of prothorax but patch of setae of trochanters diffuse. Meso- and metafemora yellow, annulated with brown; longer and narrower than profemur. Meso- and metatibiae yellow, annulated with brown; longer than protibia; metatibia with apical, pectinate row of spines on posterior surface. Meso- and metatarsi yellowish brown, longer than protarsus; meso- and metatibiae and tarsi flattened on anterior and posterior surfaces, furnished with row of swimming hairs on inner and posterior surfaces (inner row not readily apparent on mesotarsus), best developed on metathoracic legs, extending to distal area of respective femora (not shown in illustrations); tarsi 2-segmented, 1st segment very small, the 2 claws of equal length.



Figs. 7, 8. Immature stages of *B. lutarium*. 7. Fourth instar. 8. Fifth instar.

Abdomen yellow dorsally with brown maculations, and yellowish white spot at anterolateral corner of segments 3–7 that slightly overlaps preceding segment, and yellowish-white spot posteriorly near inner edge of lateral ¼ of same segments. Yellow ventrally with brown maculations and yellowish-white spots corresponding to those of dorsal surface; surface covered with long hairs, greatly convex in middle ⅓; 7 pairs of spiracles evident, 1st pair more medially placed and hidden by metacoxae.

2nd instar (Fig. 5). Length, 6.88 ± 0.05; width, 3.72 ± 0.03. Head markings dorsally similar to those of 1st instar or chevron color blending with posterior U-shaped mark.

Synthlipsis ca. 1.6× width of eye. Color ventrally similar to that of 1st instar, or brown with yellowish spot posteriorly or yellow with brown areas greatly reduced. Antennae 4-segmented, directed posteriorly, segment 1 short, ca. ½ length of 2, segments 2 and 3 subequal, each ca. ¼ length of 4. Beak varying from yellow to brown with yellow markings.

Thoracic notal color similar to that of 1st instar or brown with yellow maculations. Mesonotum ca. equal in length to pronotum along midline, posterior margin subtruncate medially and arcuate laterally; ratio of mesonotal wing pad to metanotum along lateral edge 3:2. Thoracic pleural color similar to that of 1st instar or varying from almost completely yellow to predominantly brown. Thoracic sternal color similar to that of 1st instar or with brown areas more limited.

Prothoracic leg color similar to that of 1st instar or coxa and trochanter brown and profemur brown with yellow maculations. Protibia and tarsus yellow, annulated with brown. Meso- and metathoracic leg color similar to that of 1st instar or femur and tibia brown with yellow annulations and tarsi brown. Metatibia with short, pectinate row of spines just proximal to apical row on posterior surface, proximal row ca. ½–⅔ length of apical row.

Abdominal color similar to that of 1st instar or brown with yellow maculations, anterolateral and inner yellowish-white spots usually present in both color forms, inner spots sometimes lacking in dark individuals.

3rd instar (Fig. 6). Length, 8.56 ± 0.11; width, 4.81 ± 0.05. Antennal segments 1, 2, and 3 subequal, each ca. ½ length of 4; small lateral lobe apparent on each of segments 2 and 3. Ratio of mesonotal wing pad to metanotum along lateral edge 2:1. Prothoracic leg occasionally marked with red on inner and outer surfaces. Profemur often with 2–3 brown spots on inner and outer surfaces. Metatibia with proximal pectinate row of spines of 2nd instar now longer, subequal to apical row. Interior yellowish-white spots of abdomen occasionally more obscure in dark form.

4th instar (Fig. 7). Length, 13.72 ± 0.13; width, 7.48 ± 0.05. Intersegmental line between antennal segments 3 and 4 apparently incomplete; lateral lobe of segments 2 and 3 longer, each ca. 3/4 length of 4. Mesonotum ca. 1.2× length of pronotum along midline, posterior margin subtruncate to obtuse medially and arcuate laterally; ratio of wing pad to metanotum along lateral edge 5:1. Procoxa and trochanter color similar to that of earlier instars or with occasional longitudinal red streak on outer surface of procoxa. Profemur generally with 3 brown spots on inner and outer surfaces, occasionally streaked with red. Protibia and tarsus yellow, annulated with brown or reddish brown. Meso- and metathoracic legs similar in color to those of earlier instars, in dark form tarsi brown or yellow and brown. Metatibia with 2 parallel, pectinate rows of spines proximal to apical row, basal row sometimes split or fragmented; vertical row of setae present proximal to the 2 rows.

5th instar (Fig. 8). Length, 18.52 ± 0.30; width, 10.25 ± 0.14. All antennal segments visible; lateral lobe of segments 2 and 3 longer, each subequal in shape and size to 4. Mesonotum ca. 1.3× length of pronotum along midline, posterior margin subacute medially and arcuate laterally. Wing pads of meso- and metanota (present but covered by those of mesonotum) extending to abdominal segment 2 laterally. Procoxa occasionally streaked with red on inner and outer surfaces. Profemur generally with 3 brown spots and red longitudinal streak on inner and outer surfaces. Protibia and tarsus yellow, annulated with brown or reddish brown, both segments occasionally tinged with red. Metatibia with 2 parallel, pectinate rows above apical row, both rows generally longer than in 4th instar and broken; vertical row of setae longer. Inner yellowish spots of abdomen more obscure in all forms.

ACKNOWLEDGMENTS

We thank S. L. Keffer, P. P. Korch, and T. E. Vogt, Department of Zoology, SIU-C, for their help with various aspects of this project, and Karen A. Schmitt, Scientific Photography and Illustration Facility, SIU-C, for the final illustrations of the life cycle figures and photographs of all figures. We are also grateful to J. L. Barnard, National Museum of Natural History, Washington, D.C., for identifying the amphipod used in this study.

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NAUCORIDAE (HETEROPTERA) OF NEW GUINEA. III. A REVIEW OF THE GENUS *TANYCRICOS* LA RIVERS, WITH THE DESCRIPTION OF A NEW SPECIES

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Abstract.—The genus *Tanycricos* La Rivers is reviewed based on recent collections from Papua New Guinea. A new species, *T. froeschneri,* is described, and a new key to species is provided, accompanied by illustrations of the male and female genital structures and abdominal tergites.

The genus *Tanycricos,* endemic to the mountains of New Guinea, was originally proposed by La Rivers (1971) to hold four species: *T. acumentum, T. binarius, T. longiceps,* and *T. usingeri.* Although La Rivers provided a key to his species, he employed highly variable external characters, notably the dentation on the ventral keel of the head, and provided few useful illustrations. During our recent collecting in Papua New Guinea, supported through a grant from the National Geographic Society, we obtained large numbers of *Tanycricos,* including examples of a new species, *T. froeschneri,* described herein. A search for additional characters useful in species separation revealed that the male left parameres were distinct and diagnostic, as were the structure of the female subgenital plate and the shapes of the posterior abdominal tergites in both sexes. All of these structures are illustrated, accompanied by a new key to species.

Tanycricos species are the largest naucorids found in New Guinea and form a major component of the benthic fauna in cold, rushing mountain streams above 1,500 meters elevation. Their preferred habitat is under large stones in swiftly flowing waters, where they may often be present in extremely high densities, representing the most common invertebrate predators. Individuals were observed preying on aquatic Lepidoptera larvae and were also frequently taken with immatures of a large predaceous baetid mayfly, although they were not observed feeding on the latter. In the Bulolo River at Wau teneral individuals were taken near shore in relatively slack water among cobbles, suggesting that the insects may leave their midstream habitats to molt.

Tanycricos, which was included by La Rivers (1971) in the subfamily Cheirochelinae, shares certain head characters, such as the projecting anteclypeus and posteriorly produced vertex, typical of that group. However, this genus and the closely related *Idiocarus* Montandon, exhibit clear differences from the Asian genera held in this subfamily, including slender filiform antennae, asymmetical male parameres, a well-developed labrum, and ovate pressure receptors on the thoracic venter. The New Guinean naucorid fauna is entirely endemic and, with the exception of *Aphelocheirus pallens* Horvath, appears to have radiated from a single stock. It is most closely allied to the fauna of the Philippines, but lacks many Asian elements, notably

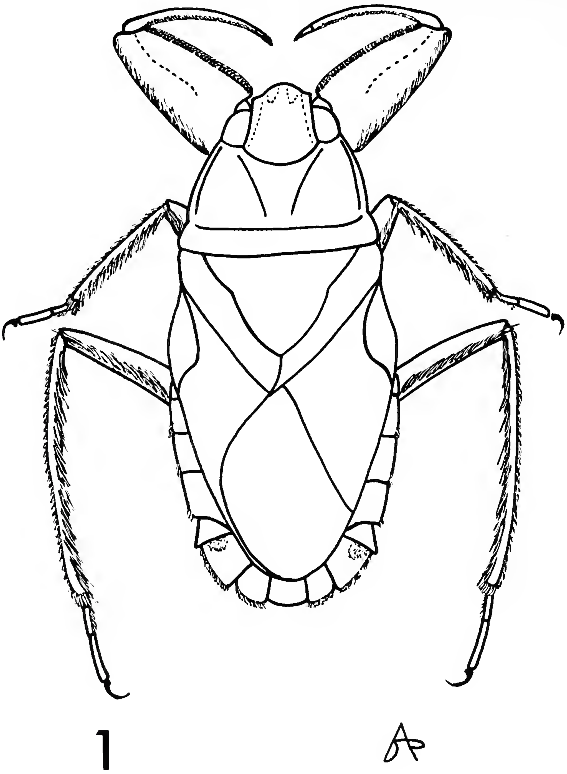


Fig. 1. *Tanycricos froeschneri* ♂, dorsal habitus.

Laccocorinae, present in that archipelago. Cheirocheline naucorids are unknown from either Celebes or the Greater Sunda islands, and further collecting in these regions will be necessary before the zoogeography and dispersal of the group, and the historical origins of the New Guinean fauna, can be accurately assessed.

All measurements and proportions are given in millimeters. CL numbers are codes referring to the authors' ecological notes. Specimen depository abbreviations are as indicated in the acknowledgments.

KEY TO THE SPECIES OF *Tanycricos* LA RIVERS

Note. When determining the number of a given abdominal tergite, count backward from the first visible tergite anteriorly. In most Naucoridae the actual tergite I is hidden beneath the metathorax.

1. Females with left posterolateral angle of abdominal tergite V, as viewed from above, distinctly produced and asymmetrical (Figs. 7, 8), posterolateral angles of abdomimal tergite VI not spinose, males with lateral projections of abdominal tergite VI extending beyond lateral margins of corresponding paratergite when viewed from below 2
– Females lacking strong asymmetry on abdominal tergite V; if weak asymmetry present,

then posterolateral angles of tergite VI spinose (Figs. 9–11); males with lateral projections of abdominal tergite VI not exceeding lateral margins of corresponding paratergite when viewed from below 3

2. Anterior margin of anteclypeus distinctly sinuate, with weak indentations present on either side of apex; middle tibia with erect slender spines present on inner face; medial hump on male abdominal tergite VI not indented apically (Fig. 12); male left paramere becoming very slender distally (Fig. 12); female abdominal tergite V strongly asymmetrical (Fig 7); female subgenital plate bifurcate for half its length, bifurcation narrowing basally (Fig. 17) .... *acumentum* La Rivers

– Anterior margin of anteclypeus evenly rounded, lacking indentations; middle tibia without erect spines on inner face; medial hump on male abdominal tergite VI indented apically (Fig. 13); male left paramere blunt, not extremely slender distally (Fig. 3); female abdominal tergite V clearly asymmetrical (Fig. 8); female subgenital plate bifurcate for two thirds its length, bifurcation widening basally (Fig. 18) *binarius* La Rivers

3. Females with posterolateral angles of abdominal tergite V produced, acute (Figs. 10, 11), males with lateral projections of abdominal tergite VI rounded (Figs. 15, 16); overall length 16 mm or less 4

– Females with posterolateral angles of abdominal tergite V not produced (Fig. 9); males with lateral processes on abdominal tergite VI squared off (Fig. 14); overall form very large and robust, length exceeding 17 mm; male left paramere tapering, tip rounded (Fig. 4); female subgenital plate bifurcate for half its length, narrowing markedly toward apex (Fig. 19) .... *usingeri* La Rivers

4. Posterolateral angles of female abdominal tergite VI acute, pointed (Fig. 10); males with distinct hump medially on posterior margin of abdominal tergite VI (Fig. 15); male left paramere acuminate distally (Fig. 5); female subgenital plate tapering evenly from base to apex, with basally widened bifurcation (Fig. 20) .... *longiceps* La Rivers

– Posterolateral angles of female abdominal tergite VI rounded (Fig. 11), males lacking medial hump on posterior margin of abdominal tergite VI (Fig. 16); male left paramere broad, blunt, not acuminate distally (Fig. 6); female subgenital plate narrowing markedly on apical half, lacking basally widened bifurcation (Fig. 21) ..... *froeschneri,* new species

Tanycricos acumentum La Rivers

Figs. 2, 7, 12, 17

Tanycricos acumentum La Rivers, 1971, 2:5.

Diagnosis. This species of slender habitus can be recognized by the pronounced asymmetry of the female abdominal tergite I (Fig. 7) and the distinctive male left clasper. It is superficially similar to *T. binarius* but can be readily separated from that species by the sinuate anterior margin of the anteclypeus, which bears indentations on either side of the apex.

Discussion. This species was described from a series of specimens taken by the Netherlands New Guinea Expedition at "Juliana Bivak," a camp below Juliana Top, the highest peak in the Star Range in what is now the Indonesian province of Irian Jaya. We have examined the holotype, a brachypterous female, and the allotype, a brachypterous male, along with three paratypes, a brachypterous female, a macropterous female, and a brachypterous male, all housed at Leiden.

T. acumentum is widely distributed in the central highlands of New Guinea along the Wahgi-Sepik divide and west into the highlands of the Trans-Fly Region. Near Mt. Hagen it was the most common species encountered in the mountain streams.

We have seen no examples of this species from the eastern third of the island, including the Markham River drainage and the Owen Stanley Range, where a variety of other congeners appears to replace it. A specimen at hand from Mendi bears the note "trout stomach contents," indicating that this species may provide a food source for these introduced fish.

Material examined. INDONESIA. **Irian Jaya:** 2♂♂, 3♀♀, Juliana Bivak, Star Mountains, 1,800 m, IX-10-59, Netherlands New Guinea Expedition (type series, RNHL). PAPUA NEW GUINEA. **Western Highlands Province:** 11♂♂, 3♀♀, upper Kaugel River, nr. Alkena, IX-7-83, CL 1786; 5♂♂, 10♀♀, Ambugla River at Tambul, IX-7-83, CL 1788; 9♂♂, 8♀♀, 8 nymphs, Pindu River nr. Alkena, IX-7-83, CL 1785; ♀, stream nr. Kiripia, IX-7-83, CL 1787; 2♂♂, ♀, 1 nymph, upper Lai River, 15 km W of Wabag Mendi Rd jct., IX-7-83; CL 1789; 3♂♂, stream 25 km W of Mt. Hagen on E side Murmur Pass, IX-7-83; ♂, ♀, stream 17 km N of Mt. Hagen on Baiyer River Rd, IX-6-83, CL 1780 (all of the above collected by J. T. and D. A. Polhemus, in JTPC). **Southern Highlands Province:** ♂, Mangani River at Mendi, IX-12-70, trout stomach contents (BPIK). **Eastern Highlands Province:** 17♂♂, 15♀♀, Goroka, VI-30-69, I. La Rivers (CAS).

Tanycricos binarius La Rivers
Figs. 3, 8, 13

Tanycricos binarius La Rivers, 1971, 2:8.

Diagnosis. This species is the smallest in the genus, with an overall length of approximately 12 mm, and can be distinguished by its size, the medial indentation on abdominal tergite VI in males (Fig. 13), the asymmetrical abdominal tergite V in females (Fig. 8), the distinctive male left paramere (Fig. 3), and the female subgenital plate with a bifurcation widening basally (Fig. 18).

Discussion. This species, described from the Herzog Mountains of Morobe Province in eastern Papua New Guinea, is extremely uncommon in collections. We have examined the type, a brachypterous female housed in the British Museum, and two paratypes, a brachypterous female and a macropterous male in the California Academy of Sciences. Although La Rivers (1971) stated that all known specimens are brachypterous, the one male paratype has fully developed wings.

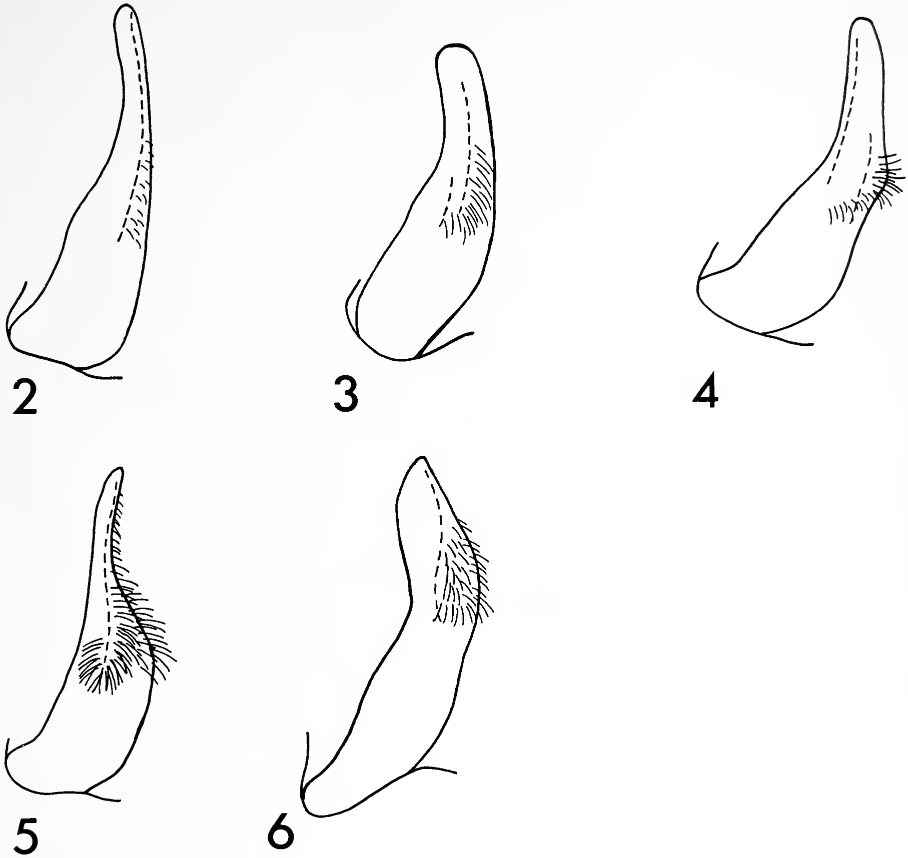
All specimens of *T. binarius* we have seen came from localities lying at over 1,200 m. The scant records indicate that this species may be widely distributed in the central ranges, but rarely collected due to its occurrence at higher elevations.

Material examined. PAPUA NEW GUINEA. **Morobe Prov.:** ♂, 2♀♀, Vagau (Wagau), Herzog Mountains, 1,219 m, January 4–17, 1965, Stn. #147, M. E. Bacchus (type series, BMNH, CAS). **Madang Prov.:** ♂, Mt. Wilhelm, X-14-57, J. H. Barrett (DPIK).

Tanycricos usingeri La Rivers
Figs. 4, 9, 14, 19

Tanycricos usingeri La Rivers, 1971, 2:13.

Diagnosis. This massive species, the largest in the genus, can be recognized immediately by its broad, robust habitus, the squared lateral projections on abdominal



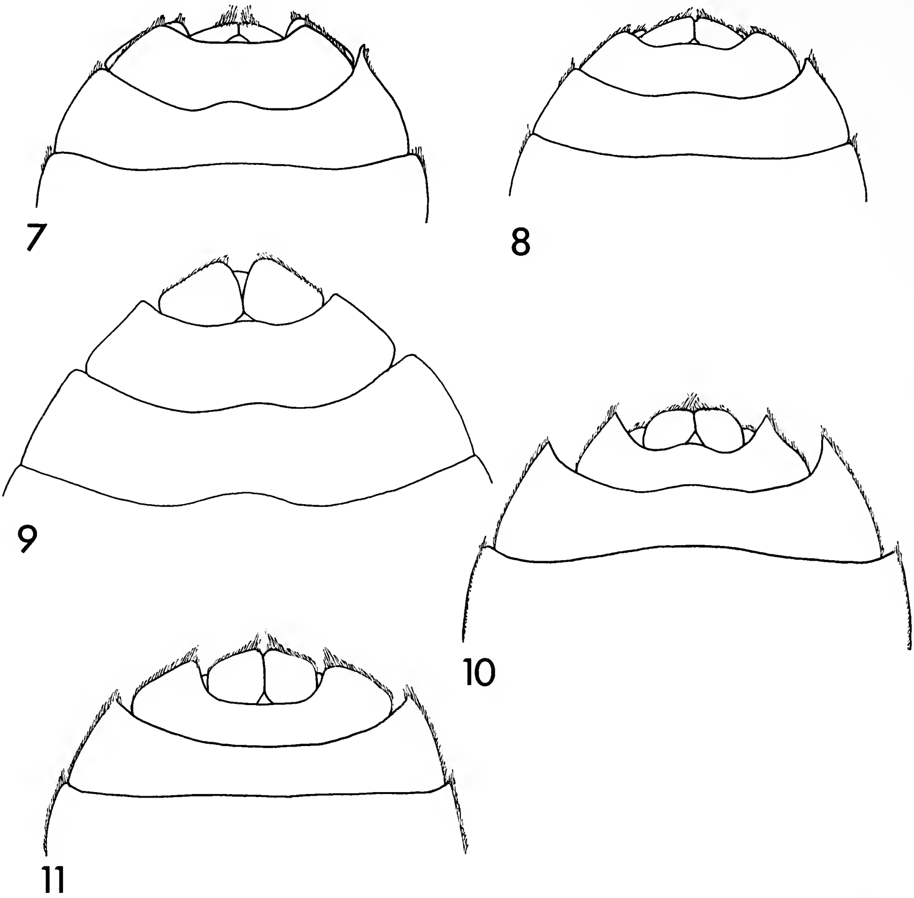
Figs. 2–6. *Tanycricos* species, male left parameres. 2. *acumentum.* 3. *binarius.* 4. *usingeri.* 5. *longiceps.* 6. *froeschneri.*

tergite VI in males (Fig. 14), the nonspinose and symmetrical abdominal tergite V in females (Fig. 9), the distinctive male left paramere (Fig. 4), and the form of female subgenital plate (Fig. 19).

Discussion. A macropterous female specimen in the British Museum bears a La Rivers label reading "*Tanycricos magnus* Paratype"; this is a manuscript name and has no validity.

T. usingeri is widely distributed in the central mountains, from the Purari drainage eastward to the Owen Stanley Range. We have no records from the upper Fly system or westward into Irian Jaya.

Material examined. PAPUA NEW GUINEA. **Western Highlands Prov.:** 6♂♂, 2♀♀, 11 nymphs, stream 27 km N of Mt. Hagen on Baiyer River Rd, IX 6-83, CL 1780; **Morobe Prov.:** 4♂♂, 5♀♀, Kauli Creek, nr. Wau, IX-17-83, CL 1826; ♂, ♀, Clearwater Creek, nr. Wau, IX-16-83, CL 1818; 6♂♂, 3♀♀, 4 nymphs, Bulolo River at Wau, 899 m (1,950 ft), IX-16-83, CL 1815; 4♂♂, 2♀♀ 2 nymphs, Big Wau Creek at Wau, 1,036 m (3,400 ft), IX-16-83, CL 1819; ♂, Wampit River, 10.7 km N of Mumeng on Wau



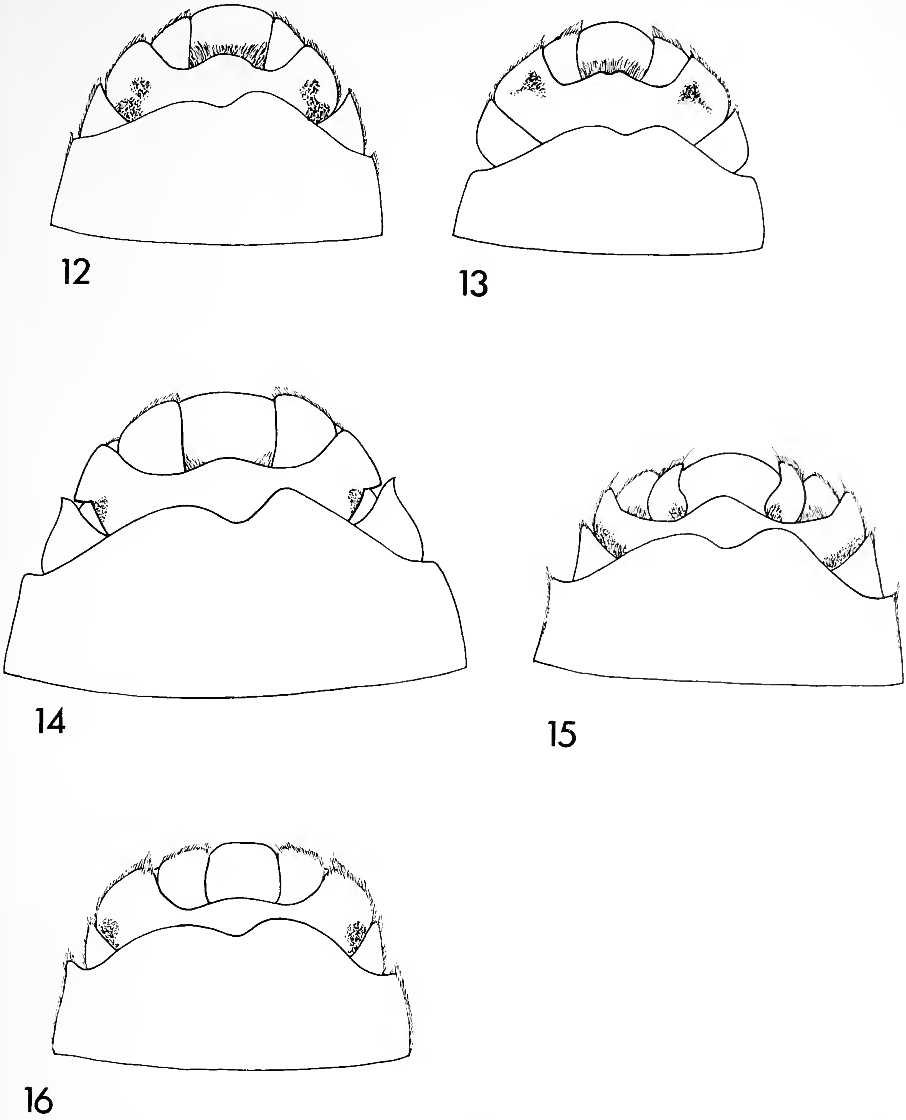
Figs. 7–11. *Tanycricos* species,female abdominal tergites V–VII. 7. *acumentum*. 8. *binarius*. 9. *usingeri*. 10. *longiceps*. 11. *froeschneri*.

Rd, IX-19-83, CL 1833 (all above collected by J. T. and D. A. Polhemus, in JTPC); 2♂♂, Bulolo River, 8 mi downstream of jct. with Karinga Creek, NW of Wau, 853 m (2,800 ft), X-12-64, W. L. and J. G. Peters (LACM). **Northern Province:** ♀, Kokoda, 366 m (1,200 ft), IX-33, L. E. Cheesman (BMNH).

Tanycricos longiceps La Rivers
Figs. 5, 10, 15, 20

Tanycricos longiceps La Rivers, 1971, 2:10.

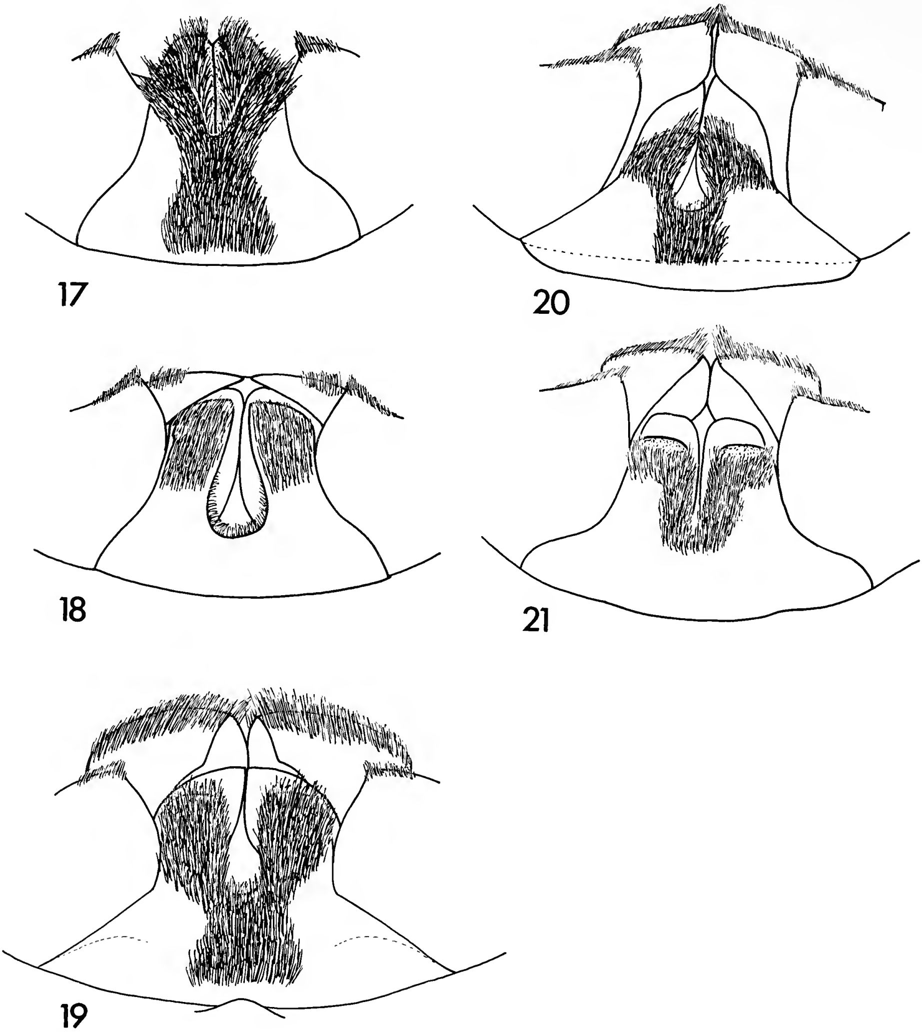
Diagnosis. T. longiceps has a slender form with a jagged aspect posteriorly, and can be recognized by the shape of abdominal tergite VI in males, with a pronounced medial hump and two blunt, tapering lateral processes (Fig. 15), the spinose posterolateral angles of abdominal tergites V and VI in females (Fig. 10), the extremely



Figs. 12–16. *Tanycricos* species, male abdominal tergites V–VII. 12. *acumentum.* 13. *binarius.* 14. *usingeri.* 15. *longiceps.* 16. *froeschneri.*

slender male left paramere (Fig. 5), and the evenly tapering female subgenital plate (Fig. 20).

Discussion. We have examined the holotype (macropterous female) and allotype (macropterous male) housed in the Bishop Museum, which were taken at light at Aiyura, in the Eastern Highlands Province of Papua New Guinea. La Rivers (1971)



Figs. 17–21. *Tanicricos* species, female subgenital plates. 17. *acumentum.* 18. *binarius.* 19. *usingeri.* 20. *longiceps.* 21. *froeschneri.*

speculated that since all the specimens at hand were winged the brachypterous form might not exist, but we have brachypterous specimens from the Bulolo River at Wau.

We have seen specimens of *T. longiceps* only from the upper Markham and Ramu drainages. Our experience indicates that this species is very local and prefers habitats in slower currents compared with its congeners. In the Bulolo River at Wau *T. longiceps* was sympatric with *T. usingeri,* but the latter occurred in midstream in areas of swift current, whereas the former was found near shore in more slowly flowing areas.

Material examined. PAPUA NEW GUINEA. **Eastern Highlands Province:** ♂, ♀, Aiyura, 1,620 m (5,313 ft), October 19–24, 1959, at light, T. C. Maa (types, BPBM). **Morobe Province:** 14♂♂, 5♀♀, Bulolo River at Wau, 899 m (1,950 ft), November 16, 1983, CL 1815, J. T. and D. A. Polhemus (JTPC); 4♂♂ ,3♀♀, same locality, October 25, 1964, W. L. and J. G. Peters (LACM, JTPC); 2♂♂, ♀, Bulolo River, 8 mi downstream of jct. with Karinga Creek, NW of Wau, 853 m (2,800 ft), October 12, 1964, W. L. and J. G. Peters (LACM); ♀, Big Wau Creek at Wau, 1,036 m (3,400 ft), October 10, 1964, W. L. and J. G. Peters (LACM); ♂, Mt. Missim, 870 m (2,853 ft), December 1, 1969, J. Sedlacek (JTPC).

Tanycricos froeschneri, new species

Figs. 1, 6, 11, 16, 21

Diagnosis. Tanycricos froschneri is superficially similar to *T. longiceps* La Rivers, but can be recognized by its thickened, gently curving male left paramere (Fig. 6), the female subgenital plate with a bifurcation that narrows basally (Fig. 21), and the structure of the male and female abdominal tergites (Figs. 10, 15), as described in the key.

Description. Macropterous form: Large, elongate (Fig. 1), basic coloration yellowish brown shaded with fuscous and black. Male length 13.63; maximum width (across abdomen) 6.34; female length 13.82; maximum width (across abdomen) 6.82; males shorter and narrower, with abdomen less expanded posteriorly.

Head yellowish brown, darker medially, adjoining lateral margins, and at base of anteclypeus, width/length = 3.18/1.73; eyes brown, shining, rounded, protrusive, convergent anteriorly, posterior/anterior interocular width = 2.27/1.82, separated from vertex by deep furrows; anteclypeus with a pair of depressions basally to either side of midline, anterior margin with slight indentations on either side of apex, greatly produced, projecting far over base of labrum, labrum subtriangular, rounded, yellowish, maxillary plates well developed, horizontally oriented, anterior margins upturned vertically along margin of rostral cavity; antennae slender, yellowish, tip of segment IV barely exceeding lateral eye margin; vertex well produced posteriorly behind eyes, margin evenly rounded.

Pronotum yellowish brown, mottled with darker brown, depressed medially behind vertex of head, width/length (midline) 5.05/2.02, lateral margins sinuate, weakly explanate, posterior margin delineated by a deep furrow, anterolateral angles sharp, pointed. Scutellum dark brown to black, width/length (midline) 3.54/2.27, lateral margins weakly sinuate. Wings fully developed, extending to posterior margin of abdominal segment VI, embolium, clavus, and corium well defined, surface set with fine granular microstructure, coloration blackish brown, with yellowish areas basally and adjoining membrane on corium, along lateral embolar margins, and at claval suture; membrane black, shining, venation obscure, surface set with fine granular microstructure.

Abdomen with lateral portions of segments I–VII exposed, brown, segments VI and VII yellowish; lateral margins of all segments fringed with short, stiff, gold setae and long, fine, recumbent, gold setae; posterolateral angles of tergite V in female produced (Fig. 11); posterolateral angles of tergite IV in male projecting well beyond lateral margins of tergite VI, tergite VI with lateral processes rounded, lacking a large medial hump (Fig. 16).

Ventral surface brown, head and medial portions of thoracic plates with covering of long, shining, recumbent, gold setae; head with prominent medial keel bearing small pointed teeth at both ends, prosternum with distinct medial carina, produced into an erect vertical keel anteriorly; proepimeron bearing elongate golden sense organ set inside lateral margin behind anterolateral angle, mesosternal plate lacking a medial carina, anterior margin not reflexed, covered with fine, golden, hydrofuge pile, lateral portions bare; mesepimeron, metasternum, and metepimeron bare, lacking hydrofuge pile; abdominal paraterites I–VI with scattered glabrous depressions in the hair pile, 1–6 per segment, consisting of a large ovate depression near inner margin, several smaller depressions adjoining spiracle, and a small depression near anterolateral margin, spiracles marked by slightly raised hair clumps, roughly ovate patches of differently reflecting hairs present laterally outside spiracles. Legs yellowish brown, posterior femora and tibiae darker; anterior femora dotted with brown dorsally, posterior margin defined by a dark tuberculate ridge set with long golden setae, anterior margin black, set with thick fringe of short gold setae; anterior tibia slender, gently curving, bearing single tarsal segment and claw; middle and posterior coxae with single raised dark tubercle apically; middle and posterior femora with paired longitudinal rows of short dark tubercles along posterior margins; middle and posterior tibiae thickly set with short reddish spines, five to six transverse rows of stout spines present apically; middle tibia bearing a longitudinal row of about seven long, slender, erect spines along inner face; middle and posterior femora, tibiae, and tarsi set with long, golden swimming hairs; claws yellowish, sharply bent, tips black, parempodia setiform.

Female subgenital plate trapezoidal, narrowing rapidly on apical half, deeply and broadly cleft for half its length, bifurcation narrowing basally (Fig. 21); male parameres asymmetrical, left paramere gently curving, broad, blunt (Fig. 6).

Brachypterous form: Similar to macropterous form in general size, structure, and coloration, with following exceptions: coloration lighter, more yellowish, especially on abdomen and hemelytra; pronotum less massive, more quadrate, posterolateral angles weakly produced; scutellum reduced, less swollen, with a furrow behind anterior margin; wings abbreviated, apices squared off, reaching only to posterior margin of abdominal segment III.

Discussion. The type series was taken from beneath large rocks in the cold, rushing waters of Gurakor Creek just upstream from the Wau road bridge. A similar habitat prevailed at the Wampit River locality, with the insects found in great numbers among the rocky, interbraided river channels of this mountain stream. We know this species only from these two localities, both of which are in the same drainage system in the upper Markham River catchment. La Rivers (1971) listed specimens of *T. longiceps* from Gurakor Creek; we have not examined this material but suspect that it may represent *T. froeschneri.* Our collections at this locality did not produce any examples of the former species, while the latter was abundant, in company with *T. usingeri* La Rivers, a pattern repeated at the Wampit River. By contrast, in the Bulolo River at Wau, *T. longiceps* was abundant, again in company with *T. usingeri,* but *T. froeschneri* was absent.

Etymology. This species is named in honor of Richard C. Froeschner, who has made valuable contributions to our understanding of hemipteran systematics.

Holotype. ♂, allotype ♀: PAPUA NEW GUINEA, **Morobe Province,** Gurakor Creek, along Wau Rd, September 15, 1983, CL 1814, J. T. and D. A. Polhemus (BPBM).

Paratypes. PAPUA NEW GUINEA. **Morobe Province:** 11♂♂, 16♀♀, 15 nymphs, same data as holotype (JTPC); 32♂♂, 29♀♀, 4 nymphs, Wampit River, 10.7 km N of Mumeng along Wau Rd, September 19, 1983, CL 1833, J. T. and D. A. Polhemus (JTPC).

ACKNOWLEDGMENTS

We thank the following individuals for the opportunity to examine specimens under their care (abbreviations following institutional names are those used in the text): Dr. P. H. Arnaud, California Academy of Sciences, San Francisco (CAS); Dr. C. L. Hogue, Los Angeles County Museum (LACM); W. R. Dolling, British Museum (Natural History), London (BMNH); Dr. P. H. van Doesburg, Rijksmuseum Van Natuurlijke Historie, Leiden (RNHL); Dr. J. W. Ismay, Dept. of Primary Industry, Konedobu, Papua New Guinea (DPIK); Dr.W. C. Gagne, Bernice P. Bishop Museum, Honolulu (BPBM). All additional material is held in the J. T. Polhemus collection, Englewood, Colorado (JTPC); types of the new species are deposited in the Bishop Museum.

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J. New York Entomol. Soc. 94(2):174–179, 1986

TWO NEW SPECIES OF *APRONIUS* STÅL WITH NOTES ON THE GENUS (HETEROPTERA: REDUVIIDAE: STENOPODAINAE)

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Abstract.—Two new species of *Apronius, froeschneri* and *granulosus,* are described as new and a key is provided for the five species now included in the genus.

Specimens loaned to me for study by the late French hemipterologist Dr. A. Villiers included one species of *Apronius* that I describe as new. Specimens in my collection included a second new species also described herein. This latter material suggests that further collecting might prove that some records of *A. flavidus* and/or *A. rapax* from the northern part of South America could be referred to still another undescribed species.

The key given below was developed from a draft originally designed by Dr. R. C. Froeschner. I want to express my appreciaton to Dr. Froeschner for his usual excellent suggestions and unending fresh ideas. It is a pleasure to name one of the new species after him. All measurements are given in millimeters. The bibliographical notes are partial.

Apronius Stål, 1865

Apronius Stål, 1865:150 (key); Stål, 1866:167 (*A. rapax*); Champion, 1898:186 (redescription); Barber, 1929/30:152 (key), 211 (redescription); Costa Lima and Campos Seabra, 1944:507–510 (key).

Diagnosis. Barber (1930:211) gave some generic characters for recognizing *Apronius.* The following generic diagnosis modifies and expands Barber's notes so that *Apronius* can be compared with other steonpodaines at the world level.

Body somewhat and relatively flattened due to the abdomen gradually expanding to the penultimate segment, not narrow and slender; head longer than wide, somewhat or decidedly shorter than pronotum; pregenal spines at base of rostrum lacking, first rostral segment shorter than last two together, first and second segments subequal; eyes hemispherical as seen from above, in lateral view oval and almost reaching or surpassing lower margin of head, in the latter case beneath extending toward each other but not touching, glabrous; lateral postocular margins slightly and gradually converging towards collum; ventrolaterally behind eyes at most with a few small, simple setigerous spines; ventrally between eyes with two to four pairs of setigerous spines; ocelli slightly elevated; jugae short; first antennal segment shorter than head and not produced beyond insertion of second, with short sparse pilosity. Pronotum usually as wide as long, sometimes a little longer than wide, shallowly transversely depressed through middle, usually a lateral tubercle before constriction; humeral angles acute, not spined. Scutellum longer than wide, with slender, porrect apex. All tarsi 3-segmented; only protibia with apical spongy fossa; trochanter with short spines; anterior femur moderately incrassate, armed with a series of small spines. Prosternum shorter behind coxa than length of coxa. Discal cell near middle of hemelytra, hexagonal. Connexival margin entire, slightly rounded, or angularly produced; 4 or 5 abdominal sterna keeled. Body relatively densely covered with short, appressed pubescence.

Apronius keys out close to *Ocrioessa* Bergroth and *Nitornus* Stål (Barber, 1930). These last two genera also have a gradually expanding abdomen and are relatively flattened, but their connexival margins are strongly produced, lobulate, or even spiny. In Barber's key *Podormus* Stål is in the same couplet with *Nitornus*. *Podormus* does not have a spongy fossa on the protibia, whereas this is present in the three other genera.

KEY TO THE SPECIES OF *Apronius*

1. Antenniphore dorsally with an elongate (longer than diameter of second antennal segment), prostrate, blunt spine. Lateral margin of anterior pronotal lobe with a prominent oblique, conical tubercle just anterior to transverse pronotal impression; pronotum densely granulose. Abdomen with posterolateral angles of connexival segments slightly projecting as round lobes, more so posteriorly. Second antennal segment black, with distinct yellow annulus subapically and one subbasally .... *granulosus,* new species

– Antenniphore without above described spine. Lateral margin of anterior lobe with or without a very low, rounded tubercle just anterior to transverse pronotal furrow; pronotum sparsely granulose. Connexival segments not or slightly projecting. Second antennal segment nearly or quite unicolorous, without such yellow annuli 2

2. In lateral view, disc of posterior pronotal lobe conspicuously sloping upward from plane of anterior lobe (Fig. 3). Disc of anterior pronotal lobe set off from pleura by a slightly elevated, granulate, calloused line. Gula with two pairs of setigerous tubercles 3

– In lateral view, disc of posterior pronotal lobe not sloping upward from plane of anterior lobe (Fig. 1). Disc of anterior pronotal lobe curving smoothly into pleura, the dividing line weakly marked by a low, nongranulose, calloused line. Gula with three or more pairs of setigerous tubercles, the last two most prominent .... *octonotatus* Barber

3. Lateral margin of anterior pronotal lobe without wartlike tubercle anterior to pronotal impression (Fig 2). Margin of connexivum straight, posterior angles not produced. Antennal segment I more than ⅔ as long as II .... *flavidus* Barber

– Lateral margin of anterior pronotal lobe with small wartlike tubercle anterior to pronotal impression. Posterior angles of connexivum slightly produced, margin not straight. Antennal segment I about half as long as II 4

4. Length of male 17 mm; head ⅙ shorter than pronotum; eyes equal in width to interocular space; basal segment of antenna about 3 times as long as preocular margin to apex of antenniphore; antennal segment I slightly less than half as long as II; spongy fossa of protibia a little longer than tarsus .... *rapax* Stål

– Length of male 19 mm; head ⅛ shorter than pronotum; eyes narrower than interocular space; basal segment of antenna 2.7 times as long as preocular margin to apex of antenniphore; antennal segment I slightly more than half as long as II; spongy fossa of protibia half as long as tarsus .... *froeschneri,* new species

Apronius flavidus Barber
Fig. 2

Apronius flavidus Barber, 1930:212.

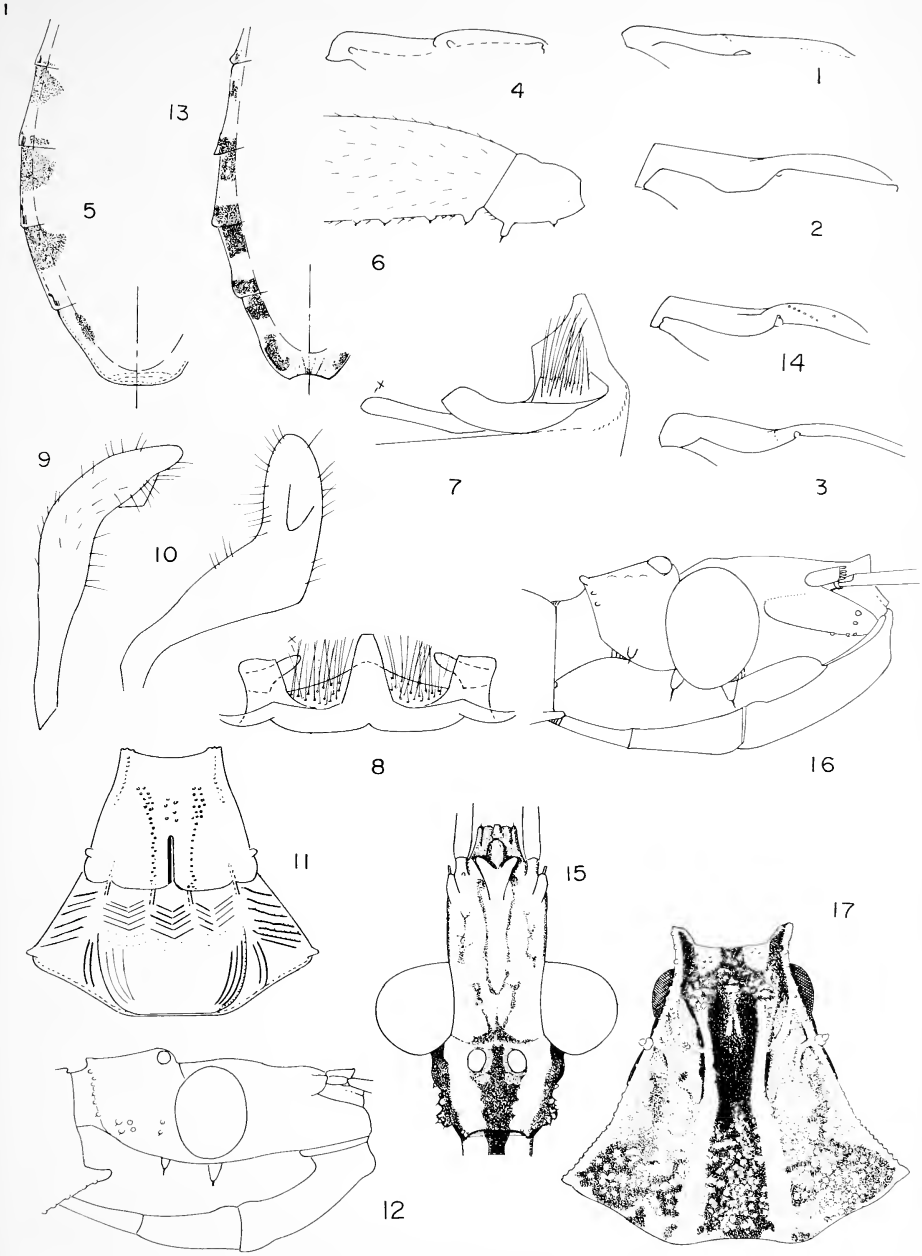
Discussion. Described from Rio de Janeiro, Brazil. Barber (1930) said "the interocular space of head is wider, the relative lengths of the antennal segments are quite different and the surface of posterior lobe is not so evidently bicarinate and is unwrinkled" as compared with *A. rapax* (Fig. 2).

Apronius granulosus, new species
Figs. 13–17

Diagnosis. Distinguished from the other species in the genus by its conspicuous whitish granulations on the thorax, the conspicuous whitish apex of cells of corium, and other characters given in the key. Genitalia not dissected in order to protect unique specimen.

Description. Male: Overall color stramineous, ornamented with brown. Head stramineous, brownish as follows: two divergent lines from interocular sulcus to base of jugae, postocellar area, interocular sulcus, laterally behind eye, and ventrally behind eyes. Laterally in front of eyes with stramineous granules. First antennal segment irregularly brownish on apical half, second antennal segment black, a postbasal and subapical yellow-stramineous annulus, third segment brown. Connexival segment basally and apically brown (Fig. 13). Beak stramineous, marked with brown as follows: first segment irregularly variegated laterally, second with a small lateral area, third with a small spot above near base. Pronotum (Fig. 17) stramineous mesally from midpoint of posterior lobe to anterior margin, and mesad from discal carinae dark brown; area between granulations on anterior part of anterior lobe and on posterior lobe brownish; granulations on anterior lobe white-yellow, longitudinal 1 + 1 discal carinae yellowish, laterally mostly yellow stramineous, darkening to brownish above acetabulum. Prosternum dark brown, grayish each side of margins of stridulatory canal; mesosternum yellowish on anterior third, posterior ⅔ dark brown and spotted with yellow where areas meet; metasternum yellowish, slightly variegated with brown. Meso- and metapleura irregularly variegated with brown over a yellow stramineous base. Hemelytra: clavus, discal cell of corium, and membrane brownish with inconspicuous lighter spots, apex of veins of corial cells distinctly yellowish white; veins of cells of membrane with light and dark brown dashes. Pro- and mesocoxae mostly yellow-stramineous, a few irregular brownish markings; metacoxa brown with a few yellowish spots; trochanters yellowish. Profemur brown above, irregularly spotted with light brown, apex yellow, below mostly yellowish-stramineous, with a preapical annulus; pro- and mesotibia with two postbasal annuli and apex dark brown; first and third tarsal segments brown, second yellowish. Meso- and metafemora yellowish, with several incomplete brownish areas spotted with yellow. Mesotibia subbasally and apically blackish. Abdomen yellowish, irregularly and abundantly spotted with yellow.

Head: from anterior margin of eye to apex of antenniphore 0.5 and to apex of head 1.1; from posterior margin of eye to neck constriction 0.7, width across eyes 2.0, interocular space above 0.7, between eyes below 0.35; gula with a pair of large



Figs. 1–17. 1. *Apronius octonotatus,* pronotum, lateral. 2. *A. flavidus,* pronotum, lateral. 3. *A. rapax,* pronotum, lateral. 4–12. *A. froeschneri.* 4. Pronotum, lateral. 5. Connexivum, dorsal. 6. Protrochanter. 7. Margin of hypopygium, lateral. 8. Same, caudal. 9. Right clasper, dorsal. 10. Same, lateral. 11. Pronotum, dorsal. 12. Head, lateral. 13–17. *A. granulosus.* 13. Connexivum, dorsal. 14. Pronotum, lateral. 15. Head, dorsal. 16. Head, lateral. 17. Pronotum, dorsal.

setigerous spines (Fig. 16); ventrolaterally behind eyes with a setigerous spine and several small granules; antenniphore dorsally with an elongate, prostrate, setigerous spine longer than diameter of second antennal segment. Jugae triangular, apex pointing upward at about 45 degrees; head with sparse, small, globular setigerous spines; gena slightly and roundly produced forward (Fig. 15). Rostral segment lengths 1.3, 1.9, 0.9. Pronotum: with granulate longitudinal carinae as in Figure 17; anterior and posterior angles sharp; length of anterior lobe 1.6, width 1.9, length of posterior lobe 1.6, width 3.5, posterior margin shallowly concave above scutellum. Prosternum with anterior angles pointed; meso- and metasternum smooth, not carinate; metapleura transversely striate. Abdomen: mesally carinate to apex of 5th sternum; connexivum with posterolateral angles slightly projecting, lobes rounded (Fig. 13). Procoxa with small setigerous spines on front and internal faces; protrochanter with 2 or 3 small setigerous spines on inner surface; femur with 9 larger, globose, setigerous spines and 2 smaller spines between each pair; spongy fossa ⅕ length of tibia; femur 3.5 times as thick as tibia (9:2.5). Length 16.2.

Holotype. ♂, FRENCH GUIANA; deposited in the Muséum National d'Histoire Naturelle, Paris.

Etymology. The trivial name refers to the heavily granulose head and pronotum.

Apronius froeschneri, new species
Figs. 4–12

Diagnosis. The characters in the key identify this species. Considering that females are usually larger than males and that this male is 19.5 mm long, this species should prove to be the largest in the genus. The contrasting dark anterior half and lighter posterior half help to allow recognition of this species. Barber's notes indicate that this contrast in coloration occasionally occurs in *A. flavidus,* a smaller species.

Description. Male: Overall coloration: head and pronotum dark brown; appendages, hemelytra, and abdomen stramineous. Head dark brown, with a diagonal, inconspicuous, pale stripe behind each eye running to collum, basal segment of antenna dark brown apically, fading to light brown toward base; antennal segment II stramineous; setigerous spines on underside of head stramineous; rostrum and collum stramineous; coxae dark brown, trochanters stramineous; profemur with an incomplete preapical brown annulus; mesofemur with preapical brown annulus; tibiae with 3 annuli, the basal pair closer to each other (hind legs missing). Scutellum dark brown. Hemelytra mostly stramineous; clavus and corium yellow-stramineous, lighter than membrane, a small dark spot on inner corial cell opposite apex of scutellum; moderately large spot on inner basal angle of discal cell and a smaller contiguous spot outside discal cell; pterostigma and membrane outside cells variegated with brownish, cell areas light brown variegated with yellowish, a small blackish dot on outer cell of membrane.

Head: Length 3.2; anteocular margin to apex of antenniphore 0.8, anteocular margin to apex of head 1.3, postocular margin to collum 0.7, length of collum 0.3, width of head across eyes 2.1, interocular space 0.7; ventrally between eyes with two pairs of moderately long setigerous spines (Fig. 12), followed by 3 small globular spines in front; jugae slightly divergent, short, upper margin horizontal. Rostral segment lengths: 1.7, 1.1, 0.8. Antennae 2.2:4.0 (segments III, IV, missing), with very short appressed setae. Ventrolaterally behind eyes with 4 or 5 small setigerous spines; large setigerous spine outside antenniphore. Pronotum: width of anterior lobe 2.1, length 1.6; width of posterior lobe 4.0, length 2.1; lateral margin of anterior lobe with small tubercle before transverse stricture; humeral angle acute (Fig. 11); lobes in lateral aspect as in Figure 4. Scutellum: width 1.5, length 1.7, length of spine 0.5, horizontal. Foreleg: trochanter apically on inner side with a moderately large setigerous spine (Fig. 6); length of femur 4.9, greatest width 1.1, armed with a single row of 12 equidistant, short, triangular, setigerous spines; length of tibia 4.0, fossa 0.7, shorter than tarsus (1:2). Genital segments as in figures 7–10. Length 19.5.

Female: Unknown.

Holotype. ♂, VENEZUELA, Rancho Grande, July 1968, at light, 1,100 m, J. Maldonado C.; deposited in the National Museum of Natural History, Washington, D.C.

Etymology. This species is named after Dr. Richard C. Froeschner, in honor of his seventieth birthday and many contributions to the study of Heteroptera.

Apronius octonotatus Champion
Fig. 1

Apronius octonotatus Champion, 1898:186, Figs. 22, 22a; Barber, 1930:213.

Discussion. Barber compared this species with *A. flavidus* and *A. rapax.* Known from Panama and British Guiana.

Apronius rapax Stål
Fig. 3

Apronius rapax Stål, 1866:167; Champion, 1898:186; Barber, 1930:211 (redescription).

Discussion. Known from Brazil, Peru, Colombia and the Canal Zone, Panama. Specimens at hand from Panama do not fit the original description; my final decision on the matter will be made after I compare this material with type specimens.

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J. New York Entomol. Soc. 94(2):180–193, 1986

NEOTROPICAL NABIDAE (HETEROPTERA), 1: A NEW GENUS, SOME NEW SPECIES, AND NOTES ON SYNONYMY

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Abstract.—A new genus *Praecarthasis* (tribe Carthasini, type species *Nabis panamensis* Harris) and seven new species are described: *Praecarthasis nigrescens* (Brazil, Peru), *P. pusillus* (Brazil), *P. paprzyckii* (Peru), *P. gibbus* (Panama, Ecuador, Peru), *P. froeschneri* (Brazil, Ecuador, Peru), *Neogorpis spinicollis* (Panama), *Alloeorhynchus alayoi* (Cuba). The following species are resurrected from synonymy: *Arachnocoris panamensis* (Distant), not a synonym of *A. albomaculatus* Scott; *Lasiomerus signatus* (Uhler) not a synonym of *L. spinicrus* (Reuter); *Hoplistoscelis sericans* (Reuter), not a synonym of *H. nigriventris* (Stål). *H. sericans* is considered a senior synonym of *H. deceptivus* (Harris) and *Alloeorhynchus moritzii* (Stein) of *A. armatus* Uhler.

The present paper contains descriptions of new taxa and notes on synonymy. The following abbreviations are used for institutions in which the material is preserved (curators who lent material are in parentheses): AMNH—American Museum of Natural History, New York (P. Wygodzinsky, R. T. Schuh); BMNH—British Museum (Natural History), London (W. R. Dolling); NRS—Swedish Museum of Natural History, Stockholm (the late E. Kjellander); UP—Department of Systematic Zoology, Charles University, Prague (P. Štys); USNM—National Museum of Natural History, Washington, D.C. (T. J. Henry, R. C. Froeschner); ZIH—Zoological Institute, Academy of Sciences of Cuba, Havana (P. Alayo D.); ZIL—Zoological Institute, Academy of Sciences of the USSR, Leningrad; ZMB—Zoological Museum, Humboldt University, Berlin, GDR (U. Göllner-Scheiding); ZMH—Zoological Museum, Helsinki University (M. Meinander). All measurements are in millimeters.

SUBFAMILY NABINAE

Tribe Arachnocorini

Arachnocoris panamensis (Distant), **Revised Status**

Fig. 3

Herdonius (?) *panamensis* Distant, 1893:419.
Arachnocoris panamensis: Bergroth, 1914:117.
Arachnocoris albomaculatus (not Scott, 1881): Bergroth, 1914:117; Myers, 1925:136–146; Harris, 1928:29.

Discussion. I have examined 6 males and 3 females of *A. panamensis* from Panama (AMNH), compared them with the holotype of *A. albomaculatus* Scott (male from Rio de Janeiro, damaged and without genital segment, BMNH), and found that the synonymy of *A. panamensis* with *A. albomaculatus*, established by Myers (1925) is incorrect. *Arachnorocis panamensis* differs from *albomaculatus* (and also from *alboannulatus* Costa Lima) by the absence of a hook on the hind trochanters in the male, by the white base of the second abdominal segment, and by the transverse white stripe on the hemelytra being wider laterally (Figs. 3–5). These species, however, do not differ in proportions of the antennal segments. The specimen on which the original description of *H. panamensis* is based, recently designated as lectotype (Carvalho and Dolling, 1976), is a female, not a male as Bergroth (1914) stated.

Tribe Carthasini

Praecarthasis, new genus

Praecarthasis (*nomen nudum*): Kerzhner, 1981:31, 34, 35, 61, 63, 82, 85.

Type species. Nabis panamensis Harris, 1926.

Diagnosis. The following features common to *Praecarthasis* and *Carthasis* differentiate them from the Nabini: long cylindrical fore coxae; fossa spongiosa placed at extreme apex of tibia; 4th antennal segment longest. The following features are intermediate between the Nabini and *Carthasis:* fore and middle tarsi 2-segmented, hind tarsi 3-segmented (all tarsi are 3-segmented in the Nabini and 1-segmented in Carthasini); forecoxal cavities closed behind but continued by a hollow for holding the coxae (they are open in the Nabini, closed and not continued by a hollow in *Carthasis*). Features common to *Praecarthasis* and Nabini but differentiating the new genus from *Carthasis:* presence of ocelli, ostiolar canals at metathorax, parastigmal pits, and Ekblom's organ (all of the above absent in *Carthasis*); moderately long rostrum (very short in *Carthasis*); fossa spongiosa only on fore and middle tibiae (on all tibiae in *Carthasis*). The following characters differentiate the new genus from both the Nabini and *Carthasis:* subdivision of corium and clavus in two parts differing in the degree of sclerotization and presence of punctures; a row of punctures at the border of ventrites II–III and III–IV; distinct punctation of abdominal mediotergites.

Description. Body elongate, nearly parallel sided or (*P. pusillus, P. paprzyckii*) slightly widened at middle of abdomen; dorsum with short setae. Body length 3.6–5.6.

Head of nearly equal length and width. Eyes large, nearly touching the hind margin of head. Ocelli large, well separated. Antennae slender, especially the last two segments; 4th segment the longest. Rostrum with 2nd and 3rd segments long and the 4th segment shortest, reaching or nearly reaching the hind coxae.

Pronotum shining, fore lobe moderately or highly raised, collar, posterior lobe of pronotum, and sides of prothorax on hind part with or without punctures. Xyphus of prothorax triangular or trapezoidal. Fore acetabulae visible from above. Forecoxal cavities set forward and closed behind, area of prothorax behind each cavity with a deep longitudinal impression for holding the coxae in repose and as a rule not visible upon casual examination. Scutellum mostly with an arcuate transverse elevation with two pits before, and often with a longitudinal elevation behind. Sides of mesothorax punctured. Metathorax with well-developed, straight, ostiolar canals of scent glands, these directed laterally and posteriorly.

Hemelytra slightly constricted on the anterior fourth, corium and clavus with typical venation, membrane without veins or with one or two straight veins near the outer margin. Base of corium and clavus (up to the level of the apex of the scutellum) more strongly sclerotized and with some punctures along the veins, the remaining part, except corium outside the R+M vein, less strongly sclerotized and as a rule more light-colored (in species of the *P. gibbus* group more or less transparent).

Fore coxae long, cylindrical, slightly thickened before base. Fore femora moderately thickened. Fore tibiae curved, shorter than femora, thickened at apex. Middle and hind coxae conical. Middle and hind femora slender. Fossa spongiosa of fore and middle tibiae well developed, arising from extreme apex of tibia. Ventral margin of fore tibiae with two rows of oblique teeth, middle tibiae without teeth. Fore and middle tarsi 2-segmented, hind tarsi 3-segmented. Claws small, simple.

Abdomen shining, covered with hairs. Mediotergites I–VII or I–VI with large punctures. Dorsal scent glands with only a single opening present between tergites III and IV in nymphs. Connexivum below not separated by a suture. Ventrites II–IV immovably fused. Border of ventrites II–III and III–IV with a row of large lateral punctures. Hind margin of sternites IV–VII (♀) or IV–VIII (♂) less sclerotized. In males of most species hind margin of sternite III with one or some black teeth at each side. Segment VIII of male covered dorsally by the preceding segment, ventrally well exposed. Ventral laterotergites IV–VII with a large parastigmal pit (fossette parastigmatique) near anterior margin, pits on segment IV smaller than the remaining. Sensory setae on last ventrites, characteristic for many Nabidae, apparently absent.

Genital segment of male as in other Nabinae, bristles of Ekblom's organ ("stridulatory organ" of early authors) in a single row. Parameres and sclerotized structures of aedeagus variable. Female with laciniate ovipositor, sternite VII with a genital apophysis, vagina symmetrical, lateral oviducts entering vagina separately, not forming a common oviduct, a single parietal gland (not found in all species) lying on the dorsal side of the vagina behind the base of vermiform gland.

Etymology. From the Latin *prae,* before, and the generic name *Carthasis.*

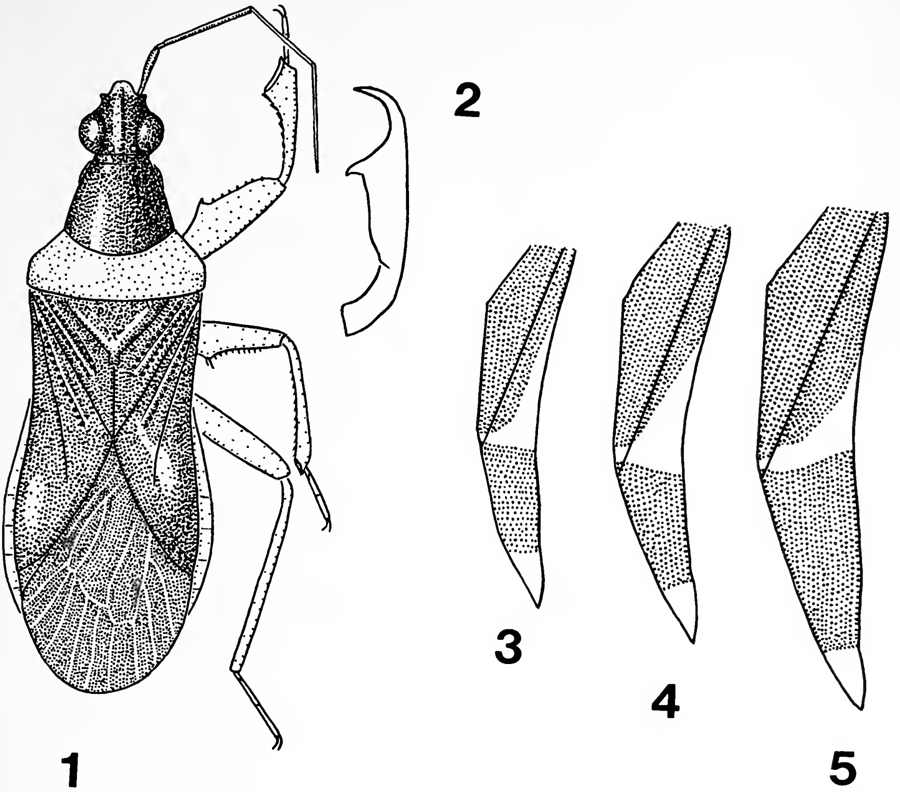
Discussion. The genus includes six species, all from tropical America. They can be subdivided in two groups. Characters of the groups are indicated in the key and omitted in the species descriptions.

Before this study the tribe Carthasini included only one genus, *Carthasis* Champion, with nearly all species found in Central America and the West Indies. Because of reduction of ostiolar canals of metathoracal scent glands some authors wrongly referred this genus to Reduviidae (Blatchley, 1926) or placed it in Nabidae with doubt (Carayon and Villiers, 1968:708). *Praecarthasis* is interesting because it has many intermediate characters between Nabini and *Carthasis* (see Kerzhner, 1981:85, on the evolution of Carthasini).

KEY TO SPECIES OF *Praecarthasis*

1. Fore lobe of pronotum moderately raised; hind lobe, collar, and sides of prothorax densely punctured (Figs. 6, 7). Third antennal segment shorter than the 2nd. Fore femora, fore tibiae, and 1st segment of hind tarsi without long bristles (Fig. 6). Xyphus of prothorax more or less triangular. The more sclerotized and punctured part of hemelytra slightly longer than scutellum, the remaining part of corium and clavus not transparent. Mediotergites I–VII of abdomen punctured. In male, sternite III of abdomen without teeth or with one tooth at each side. Body mostly yellowish, except in *P. nigrescens.* (*P. panamensis* Group) 2

– Fore lobe of pronotum humped; hind lobe, collar, and sides of prothorax not punctured, or only the hind lobe with 1–2 rows of punctures on fore margin (Figs. 8, 9). Third



Figs. 1–5. 1, 2. *Alloeorhynchus alayoi.* 1. Female. 2. Paramere. 3. *Arachnocoris panamensis,* clavus and corium of male. 4. *A. albomaculatus,* the same. 5. *A. alboannulatus,* the same.

antennal segment longer than the 2nd. Basal half of fore femora with two long setae, the basal one stouter and darker; fore tibiae on ventral side with 2 rows of bristles intermixed between oblique teeth; 1st segment of hind tarsi with a long bristle at apex (Fig. 8). Xyphus of prothorax trapezoidal. The more sclerotized and punctured part of hemelytra shorter than scutellum, the remaining part of corium and clavus more or less transparent (except lateral part of corium). Mediotergites I–VI of abdomen punctured. In male, sternite III of abdomen with four or more teeth on each side. Body mostly black. (*P. gibbus* Group) 5

2. Body length subequal to or longer than 4 mm. In male, sternite III of abdomen with a tooth on each side 3
– Body length distinctly less than 4 mm. In male, sternite III of abdomen with one tooth on each side or without teeth 4
3. Head, nearly the whole pronotum, and antennae yellow. Femora with a narrow brown ring before the apex .... *panamensis* (Harris)
– Head, pronotum completely or in a great part, and 1st and 2nd antennal segments at least partly black or brownish black. Femora without brown rings .... *nigrescens,* new species
4. Femora without brown rings or spots. Hind lobe of pronotum unicolorous. In male,

Table 1. *Praecarthasis,* means of some measurements in millimeters.

	panamensis		*nigrescens*		*pusillus*	*paprzyckii*		*gibbus*		*froeschneri*	
	♂	♀	♂	♀	♂	♂	♀	♂	♀	♂	♀
Head length	0.50	0.51	0.54	0.57	0.48	0.51	0.51	0.61	0.64	0.50	0.52
Head width	0.50	0.50	0.60	0.62	0.51	0.50	0.50	0.69	0.72	0.57	0.60
Vertex width	0.17	0.16	0.19	0.20	0.20	0.19	0.19	0.26	0.29	0.23	0.23
Length antennal segment I	0.57	0.59	0.64	0.63	0.52	0.56	?	0.65	0.66	0.47	0.49
Length antennal segment II	0.73	0.73	0.79	0.79	0.60	0.67	?	0.87	0.84	0.64	0.67
Length antennal segment III	0.60	0.60	0.57	0.57	0.43	?	?	1.38	1.31	0.71	0.76
Length antennal segment IV	?	?	?	1.00	0.93	?	?	1.57	1.57	1.36	1.43
Length rostral segment II	0.57	0.60	0.64	0.66	0.57	0.54	0.54	0.90	0.89	0.71	0.79
Length rostral segment III	0.43	0.44	0.46	0.50	0.40	0.44	0.42	0.68	0.71	0.54	0.59
Length rostral segment IV	0.23	0.21	0.27	0.29	0.23	0.20	0.20	0.32	0.31	0.29	0.26
Length pronotum	0.87	0.90	1.06	1.11	0.86	0.93	0.94	1.16	1.21	0.90	1.01
Width pronotum	1.00	1.07	1.24	1.30	0.96	0.99	1.03	1.24	1.38	0.96	1.17
Length fore femur	1.27	1.29	1.36	1.40	1.13	1.23	1.29	1.78	1.75	1.36	1.42
Thickness fore femur	0.23	0.23	0.24	0.26	0.20	0.21	0.21	0.30	0.32	0.24	0.26
Length hind tibia	1.70	1.70	?	1.95	1.70	?	1.79	2.40	2.47	1.79	2.02

sternite III of abdomen without teeth .... *pusillus,* new species

– Femora with a brown ring or spot near the apex. Hind lobe of pronotum with three brown stripes. In male, sternite III of abdomen with a tooth at each side .... *paprzyckii,* new species

5. Hind lobe of pronotum without punctures. Length more than 4.5 mm. Fore femora, as a rule, widely brown in middle .... *gibbus,* new species

– Hind lobe of pronotum with 1 or 2 rows of punctures at fore margin. Length less than 4.5 mm. Fore femora not brown .... *froeschneri,* new species

Species of *P. panamensis* Group (see key)

Praecarthasis panamensis (Harris, 1926), **New Combination**

Figs. 6, 7, 16, 17, 26

Nabis panamensis Harris, 1926:3; 1928:46.

Diagnosis. Dirty yellow, fore corners, humeri and faint median line at the hind lobe of pronotum, apex of scutellum, and veins on the inner corner of corium and the apical third of clavus more or less brown. Corium slightly darker at middle and apex. Sides of the head behind eyes, thorax beneath, and lateral stripes at base of abdomen on underside brown. Rostrum, antennae, and legs pale yellow, antennal segment 1 and narrow subapical ring on femora brown. In male, abdominal sternite III with one tooth on each side. Paramere, aedeagus, and vagina as in Figures 16, 17, 26. Length of male 4, of female 4.1; width of male 1.1, of female 1.2.

Discussion. I have examined the holotype and the allotype, both from Porto Bello, Panama (USNM).

Praecarthasis nigrescens, new species

Figs. 14, 15, 18, 19, 27

Description. Head, except neck, black. Pronotum and scutellum in females black or blackish brown, in male the fore margin of collar, posterior two thirds of hind lobe of pronotum and lateral corners of scutellum dirty yellow. Hemelytra blackish, brownish or dark grey, in male paler at base of corium and clavus. Thorax beneath brownish black, abdomen yellow, genital segment of male and genital sclerites of female (except ovipositor itself) black. Rostrum, antennae, and legs yellow, segment 1 of rostrum and two basal antennal segments almost completely, or at least at apex, brown, femora without brown rings. In male, abdominal sternite III with one tooth on each side. Paramere, aedeagus, and vagina as in Figures 18, 19, 27. Length of male 4.4, of female 4.6–4.9; width of male 1.3, of female 1.4.

Holotype. ♂, BRAZIL, **Matto Grosso,** Sinop, 12°31′N, 55°37′W, Oct. 1975 (M. Alvarenga; AMNH).

Paratypes. 2♀♀ BRAZIL: **Para,** Jacareacanga, May 1969 (F. R. Barbosa; AMNH, ZIL); 2♀♀, PERU: **Junin,** Satipo, 10 July and 24 Aug. 1941 (P. Paprzycki; USNM).

Etymology. Named for its blackish color, from the Latin *nigrescens*, blackish.

Praecarthasis pusillus, new species

Figs. 20, 28

Description. Head dirty yellow, posterior half on dorsum with a longitudinal brown stripe. Pronotum and thorax beneath tawny. Scutellum yellow, with the apex brown or with a longitudinal brown stripe. Basal part of hemelytra light tawny, remaining part brownish gray, except veins on the inner half of the corium brown, apical half of corium outside of vein R+M tawny, dark at hind margin, area around the transverse vein between R+M and Cu dark. Membrane light gray, with one or two veins. Abdomen beneath dirty yellow. Rostrum, antennae, and legs dirty yellow, without brown spots. Abdominal sternite III in male without teeth. Paramere and aedeagus as in Figures 20, 28. Length of male 3.6, width 1.1. Female unknown.

Holotype. ♂, BRAZIL, **Rio de Janeiro,** Conceição de Macabú, Aug. 1977 (M. Alvarenga; AMNH, will be deposited in Brazil).

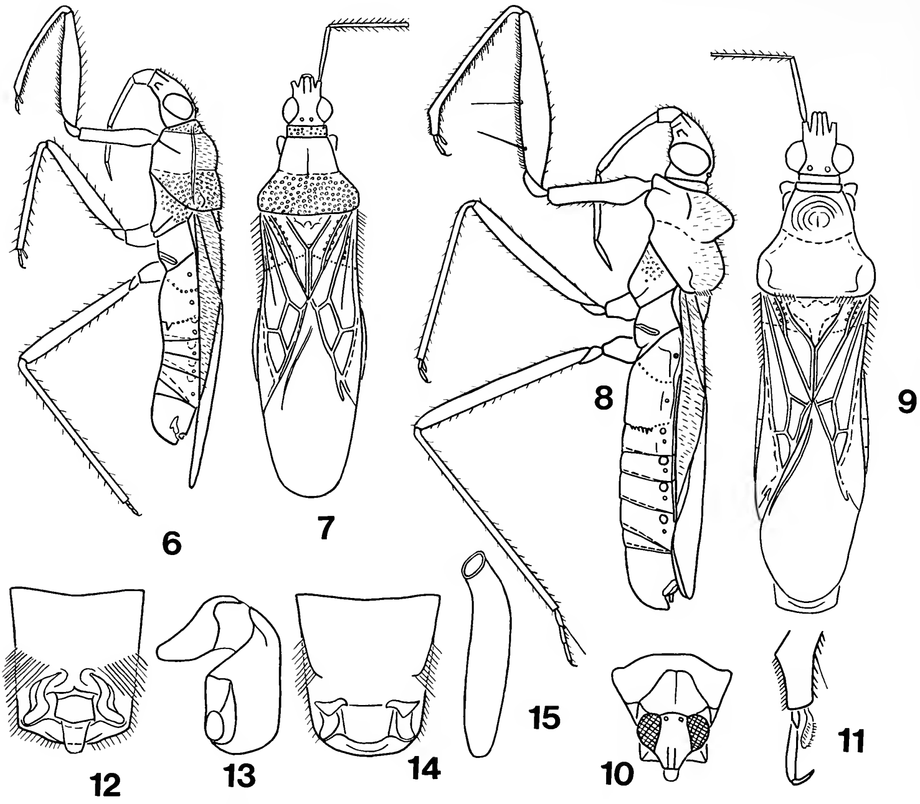
Paratype. ♂, "BRAZIL, on orchid," "S. Francisco, Cal., 24 Jan. 1941, # 17427" (USNM), specimen apparently intercepted by San Francisco quarantine inspection.

Etymology. Named for its small size, from the Latin *pusillus*, small.

Praecarthasis paprzyckii, new species

Figs. 21, 29

Description. Head dirty yellow, posterior half on dorsum brown or with a longitudinal dark brown stripe. Pronotum dirty yellow, sides of collar and fore lobe

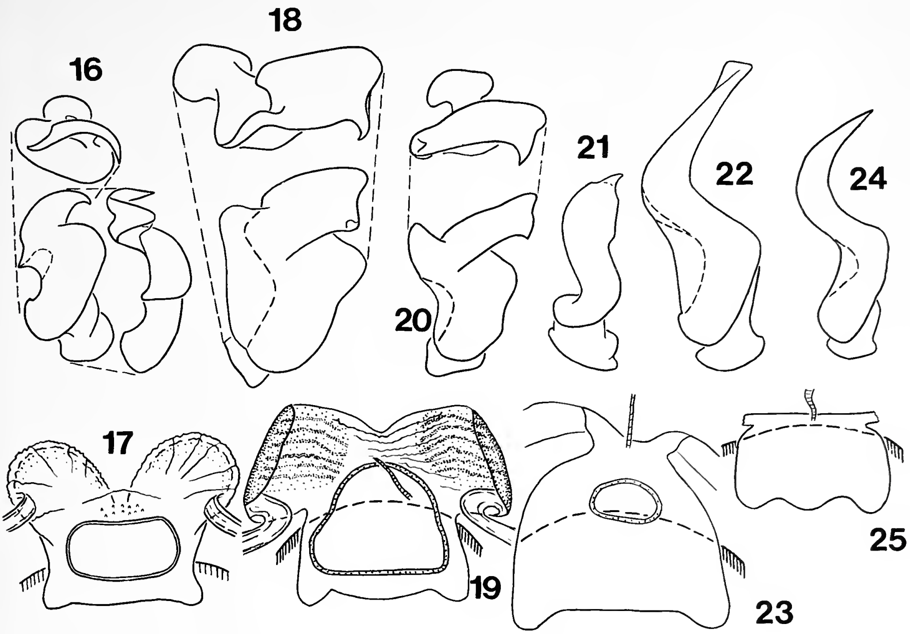


Figs. 6–15. *Praecarthasis.* 6, 7. *P. panamensis.* 6. Lateral view of male. 7. Dorsal view of male. 8–13. *P. gibbus.* 8. Lateral view of male . 9. Dorsal view of male. 10. Head and pronotum in frontal view. 11. Apex of fore tibia and fore tarsus. 12. Genital segment of male. 13. Penis. 14, 15. *P. nigrescens.* 14. Genital segment of male. 15. Ovarian egg.

brownish black, hind lobe with 3 longitudinal, brownish stripes. Scutellum yellow, with a longitudinal, blackish, brown stripe. Thorax beneath brownish black, with some parts yellowish or reddish. Basal part of corium and clavus dark yellow, with indistinct oblique brownish stripe between the veins, remaining part yellowish gray, veins in the inner part of corium, a spot from inner discal cell of corium up to its lateral margin and apex of corium brownish black. Membrane gray, with two dark spots on apical half, two veins near the outer margin. Abdomen beneath dark yellow, with two longitudinal black stripes at base, sternite III in male with a tooth at each side. Antennae, rostrum, and legs yellow, 1st segment of rostrum and a narrow subapical ring on all femora (interrupted at fore and middle femora) brown. Paramere and aedeagus as in Figures 21, 29. Vagina mutilated during preparation. Length of male and female 3.7; width of male 1.05, of female 1.15.

Holotype. ♂, PERU, **Junin,** Satipo, 9 Aug. 1941 (P. Paprzycki; USNM).

Paratype. ♀, PERU, **Huanuco,** Tingo Maria, vegetation on steep hillside 1 km SE



Figs. 16–25. *Praecarthasis.* 16, 17. *P. panamensis.* 16. Paramere. 17. Vagina. 18, 19. *P. nigrescens.* 18. Paramere. 19. Vagina. 20. *P. pusillus,* paramere. 21. *P. paprzyckii,* paramere. 22, 23. *P. gibbus.* 22. Paramere. 23. Vagina. 24, 25. *P. froeschneri.* 24. Paramere. 25. Vagina.

of town, forested eastern foothills of the Andes, 2,000 m, 15 Aug. 1971 (P. S. and H. L. Broomfield; BMNH).

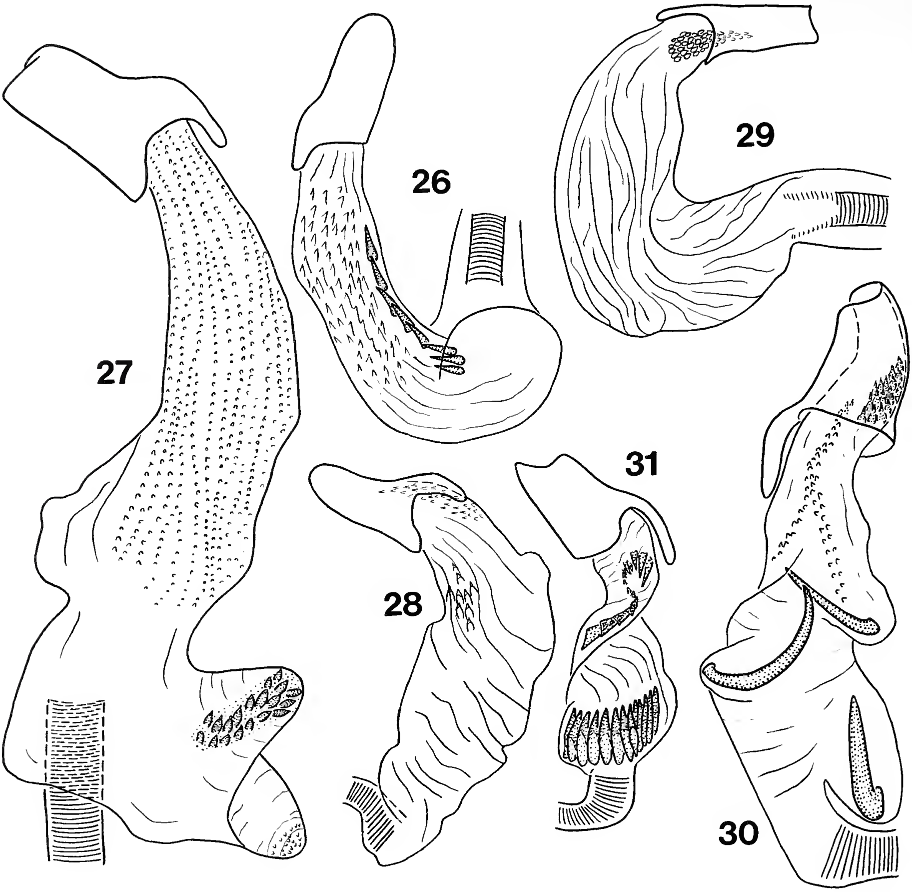
Etymology. Named in honor of P. Paprzycki, collector of the holotype.

Species of *P. gibbus* Group (see key)

Praecarthasis gibbus, new species

Figs. 8–13, 22, 23, 30

Description. Body black or brownish black, hemelytra usually slightly more light colored than head and pronotum and, in a great part, slightly transparent. Corium on the hind fourth with a white spot at lateral margin or (in some specimens from Peru) with a transverse white stripe, membrane with a white spot near the apex of corium. Abdomen beneath in the middle of segments IV–VII (♀) or IV–VIII (♂), and sometimes at lateral margins, yellow. Antennal segment 1 dirty yellow, segment 2 completely black or, at least on the apical ⅓, brown, segments 3 and 4 brown. Rostrum and legs yellow, rostral segment 1 and a wide ring in the middle of fore femora brown, darkening of femora sometimes indistinct (in some specimens from Peru). Abdominal sternite III in male with 6–7 teeth at each side, size of teeth gradually increasing to the lateral margin, except for the very small last tooth. Pronotum very shiny, without punctures. Paramere, aedeagus, and vagina as in Figures 22, 23, 30; sclerites at base of ovipositor, visible through vagina, covered with numerous small



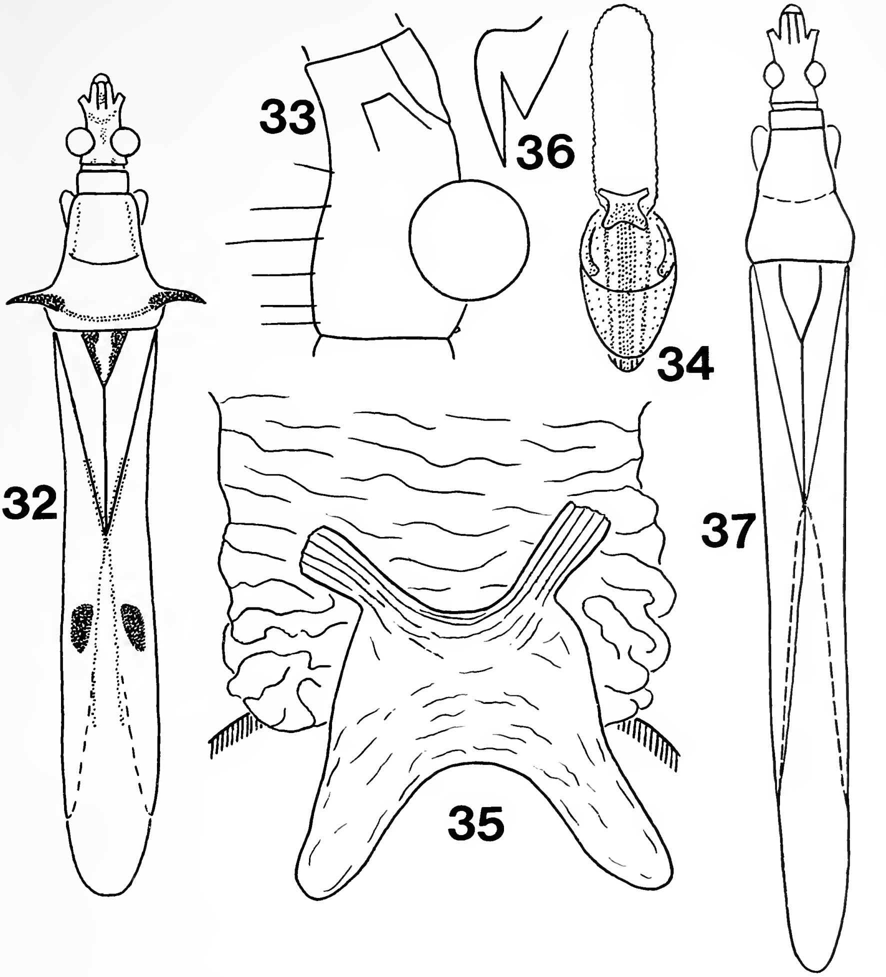
Figs. 26–31. *Praecarthasis,* aedeagi. 26. *P. panamensis.* 27. *P. nigrescens.* 28. *P. pusillus.* 29. *P. paprzyckii.* 30. *P. gibbus.* 31. *P. froeschneri.*

teeth (in this species only). Length of male 4.8–4.9, female 5–5.6; width of male 1.1–1.15, female 1.1–1.4.

Holotype. ♂, ECUADOR, **Pastaza**, Ashuara Indian Village about 10 km from Rio Morena, 14 July 1971 (B. Malkin; AMNH).

Paratypes. ECUADOR: ♀, same data as for holotype (ZIL); ♀, **Pastaza**, Rio Macuna, 10 km from Rio Morena, 300 m, 11–16 July 1971 (B. Malkin; AMNH). PANAMA: ♂, Barro Colorado I., Canal Zone (J. Zetek; AMNH). PERU: **Junin**: ♀, San Ramon de Pangoa, 40 km SE Satipo, 750 m, pl. 2, soil-litter layer in primary forest, 7 June 1972 (R. T. and J. C. Schuh; AMNH); ♂, Satipo, 10 Aug. 1941 (P. Paprzycki; USNM). **Cuzco,** ♀, Quincemil, Aug. 1962 (L. A. Peña; USNM).

Etymology. Named for its humped pronotum from the Latin adjective *gibbus,* humpbacked.



Figs. 32–37. *Neogorpis.* 32-36. *N. spinicollis.* 32. Body from above. 33. Head from the side. 34. Genital sclerites and vagina of female (same magnification as in Fig. 32). 35. Base of vagina, enlarged. 36. Claw. 37. *N. neotropicalis,* body from above.

Praecarthasis froeschneri, new species
Figs. 24, 25, 31

Description. Body black, hemelytra (except base, apex of corium, and lateral part before the white stripe) more light colored, grayish brown and transparent than in *P. gibbus.* Posterior ¼ of corium with a transverse white stripe, veins on the transparent area of hemelytra dark, except anterior area of the vein Cu. Abdomen beneath with yellow area medially on sternites III or IV to VII (♀) or VIII (♂), and often with yellow lateral margins. Rostrum, antennae, and legs yellow, segment 1 of rostrum brown, apex of antennal segment 2 light brownish. Abdominal sternite III in male with 4 teeth at each side, the size of them gradually increasing to the lateral margin, but lateral-most tooth much larger than the preceding. Pronotum in lateral aspect less shiny on collar and, sometimes, on hind lobe; fore margin of the hind lobe with one row of punctures, sometimes with a second row. Paramere, aedeagus, and vagina as in Figures 24, 25, 31. Length of male 3.9–4.4, female 4.1–4.4; width of male 0.9–1.1, female 1.1.

Holotype. ♂, ECUADOR, **Pastaza**, Ashuara Indian Village, about 1 km from Rio Morena, 14 July 1971 (B. Malkin; AMNH).

Paratypes. ♀, ECUADOR, same data as for holotype (ZIL). PERU: **Junin:** ♀, Estancia Naranjal San Ramon, 1,000 m, 20–27 July 1965 (P. and B. Wygodzinsky; AMNH); ♀, Satipo, 10 Aug. 1941 (P. Paprzycki, USNM). BRAZIL: **Mato Grosso:** ♀, Sinop, 12°31′S, 55°37′W, Oct. 1974 (M. Alvarenga; AMNH).

Etymology. It is a great pleasure for me to dedicate this species to Dr. R. C. Froeschner on the occassion of his 70th birthday and in recognition of his excellent work on Ecuadorian Heteroptera.

Tribe Gorpini

Neogorpis Barber, 1924

Diagnosis. Neogorpis differs from *Gorpis* Stål as follows: eyes subspherical (Fig. 33), highly raised above the vertex; ocelli reduced; head beneath with two rows of stout bristles; right and left sides of prothorax fused behind coxal cavities, nearly without medial suture; xyphus of prothorax more or less truncate at apex; hemelytra folded around sides of abdomen; lateral margins of abdomen raised above and partly folded over upper side; claws (Fig. 36) with a large tooth at base.

Neogorpis spinicollis, new species

Figs. 32–36

Description. Light yellow, partly greenish or with an orange hue. Humeral projections above black, holotype with an arciform brown stripe between humeral angles. Scutellum largely brown laterally or completely light brown. Clavus slightly darker along the commissure. Corium on the hind third with a small black spot nearly touching its inner margin. Diffuse reddish spots present on dorsal surface of head and near sides of fore lobe of pronotum. Border between corium and apical half of clavus and basal half of membrane marked with a narrow red stripe. All red markings reduced or absent in the Porto Bello specimen. All femora or only middle and hind femora with an interrupted, subapical, red ring.

Eyes raised above vertex by nearly half of their height. Ocellar tubercles present, but ocelli reduced. Antennal segment 1 as long as head and pronotum together. Humeral angles of pronotum projected into long, sharp spines, collar and hind lobe slightly shining, finely wrinkled and puncate, hind margin straight. Hemelytra just surpassing the apex of abdomen, hind wings not quite reaching apex.

Length 10.3–10.7, width at middle of abdomen 1.2; head length 1.05, width 0.85; distance between eyes 0.17; length of antennal segments (I–IV) 3.0, 3.8, 2.6, 1.9; length of rostral segments (II–IV) 1.2, 0.8, 0.4; pronotal length 2.0, width at hind margin 1.5, at humeral projections 2.5–2.6; length of fore femora 3.8, width 0.47, length of hind tibiae 6.3.

Vagina (Figs. 34, 35) with a long membranous bag, nearly reaching the middle of abdomen.

Male unknown.

Holotype. ♀, PANAMA, Canal Zone, Barro Colorado I. (K. Cooper, AMNH).

Paratypes. PANAMA: ♀, same locality as holotype, 27 Dec. 1940 (K. W. Cooper, AMNH); ♀, Porto Bello, Jan. 1971 (J. Maldonado Capriles; USNM).

Discussion. In *N. neotropicalis* (Barber) from Puerto Rico, the only species of *Neogorpis* known before this study (Fig. 37), the pronotum lacks humeral projections, the hemelytra are without black spots and red stripes, and antennal segments 2 and 3 and the rostrum have red spots.

Etymology. Named for the projecting humeral angles of the pronotum; from the Latin *spina,* spine, and *collum,* neck (often used for the prothorax of insects).

Tribe Nabini

Lasiomerus signatus (Uhler), **Revised Status**

Coriscus signatus Uhler, 1894:205.
Nabis signatus: Champion, 1899:304.
Reduviolus spinicrus (in part): Reuter, 1908:103.
Nabis spinicrus Harris (not Reuter, 1890): 1928:47.

Discussion. The synonymy of *L. signatus* with *L. spinicrus,* established by Reuter (1908), is incorrect. I have examined the holotype of *N. spinicrus* (brachypterous male, Brazil, ZMH) and a series of macropterous males and females of *L. signatus* from various countries, including some syntypes (Grenada Is.; USNM, ZIL). These species, in addition to some external characters, have good differences in the male genitalia.

Hoplistoscelis sericans (Reuter), **Revised Status**

Nabis sericans Reuter, 1872:83.
Nabis nigriventris: Champion (in part, not Stål, 1862), 1899:302.
Nabis deceptivus Harris, 1928: 45. **New Synonymy.**

Discussion. The lectotype of *N. sericans* is designated as follows: macropterous male in NRS labeled "Texas"; "Belfrage"; "*sericans* Reut. Typ." (O. M. Reuter's handwriting), "Typus." I also have examined paralectotypes, 3 brachypterous females labelled "Texas" and "Belfrage" (NRS, ZMH). The synonymy of *N. sericans* with *N. nigriventris,* established by Champion (1899), is incorrect, and in fact, *N. sericans* is a senior synonym of *N. deceptivus,* as suspected by Harris (1928).

SUBFAMILY PROSTEMMATINAE

Alloeorhynchus alayoi, new species

Figs. 1, 2

Alloeorhynchus sp. Alayo, 1967:4, pl. 1, fig. 1; Alayo, 1971:14.

Diagnosis. Easily distinguished from all New World species by the combination of the black fore lobe of the pronotum, the orange-yellow hind lobe, and the black hemelytra. In *A. vittativentris* Stål the fore and hind lobe are black, and the body length is 5.0. In *A. moritzii* Stein the fore lobe is black, hind lobe from black to dirty yellow, but hemelytra are yellow at the base.

Description. Very shiny, scutellum, clavus mesad of vein, inner corner of corium, and underside of metathorax dull. Entire body covered with light-colored setae.

Head except apex, fore lobe of pronotum, scutellum, hemelytra, underside of thorax (except fore acetabulae and hind part of prothorax), and basal segment of abdomen (except lateral margins) black or dark brown. All remaining parts of the body, legs, and rostrum yellow, sometimes apices of femora and connexivum tinged with pink and hind lobe of pronotum tinged with orange. Antennae dirty yellow to dark brown.

Eyes slightly narrower than vertex. Ocelli large. Antennal segment 1 slightly shorter than width of vertex plus one eye, segment 2 slightly less than twice as long as 1, segment 3 shorter than 2, segment 4 the longest. Rostrum reaching to middle of mesothorax. Pronotum 1.2 times broader than long, fore lobe twice as long as hind lobe, hind margin straight or slightly concave. Scutellum with two pits near the base, apex slightly widened and truncate. Clavus with two rows of punctures on basal ⅔, corium with a row of 13–15 punctures at each side of innermost vein (Cu). Membrane with distinct typical venation, the innermost of three cells not touching the base of membrane.

Fore femora widest slightly before the middle (nearer to the base), with two rows of about 13 black teeth, extending from widest part to the apex. Fore tibiae strongly widened on apical third. Middle femora widest in the middle, widest part with two long black teeth, hind tooth longest, positioned distally from these teeth two rows of smaller black teeth, the hind (posteroventral) row shorter, with about 6 teeth, the fore (anteroventral) row longer with about 10 teeth. Middle tibiae feebly widened toward the apex. Hind femora without black teeth. Connexivum above without spots formed by black setae.

Length of male 3.4, female 3.4–4.5; width of male 1.25, female 1.4–1.55; head width 0.57–0.64, interocular distance 0.23–0.27, pronotal length of male 0.96, female 0.96–1.21; width of male 1.14, female 1.21–1.46; length of antennal segments I–IV 0.36–0.43, 0.64–0.74, 0.57–0.64, about 0.85; length of rostral segments I–IV 0.21–0.24, 0.43–0.50, 0.30–0.36, 0.15–0.17.

Paramere as in Figure 2.

Holotype. ♂, CUBA, S.[agua] la Grande, 2 Jan. 1936 (C. G. Aguayo; ZIH).

Paratypes. CUBA: ♀, E. E. A. [Estancia Experimental Agraria] de Cuba, No. 9817, *Alloeorhynchus* n. sp.? S. C. B[runer] (ZIH); ♀, Playa Larga, C. Zapata, 1 May 1968 (P. Alayo; ZIH); ♀, Lomas de Soroa, Pinar del Rio, a la luz, May 1965 (ZIH); 2♀♀, Soledad, Cienfuegos, Las Villas, a la luz, Feb. and March 1968 (ZIH; ZIL); ♀, valley of R. Jora, 27 May 1965 (Stary; UP).

Etymology. It is a pleasure for me to dedicate the name of this species to the Cuban entomologist P. Alayo D., who published its first description and figure.

Alloeorhynchus moritzii (Stein)

Prostemma moritzii Stein, 1860:77.
Alloeorhynchus moritzii: Stål, 1873:109; Reuter and Poppius, 1901:40.

A. armatus Uhler, 1894:207; Reuter and Poppius, 1909:41; Harris, 1928:15. **New Synonymy.**

Discussion. I have examined the holotype of *P. moritzii,* a male from the island "St. Jean" (St. John) in the Virgin Islands (ZMB).

ACKNOWLEDGMENTS

I am thankful to all who provided me with material for this study (see introduction), and to the New York Entomological Society for publishing this paper without page charges.

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A MOST STRIKINGLY MYRMECOMORPHIC MIRID FROM AFRICA, WITH SOME NOTES ON ANT-MIMICRY AND CHROMOSOMES IN HALLODAPINES (MIRIDAE, HETEROPTERA)

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Abstract.—The remarkably myrmecomorphic characters of the hallodapine mirid *Leaina belua* Linnavuori from West Africa are described and illustrated and some comparisons made with other antlike mirids exhibiting supposed imitations of orthopteroid mandibles. Some literature on the possible role of ant mimicry in Miridae and Alydidae is reviewed. A plea is made for detailed observations on the biology of those hallodapines that display the highest degree of myrmecomorphy. Attention is further paid to the exceptionally low number of chromosomes (n = 2 and 4) in some hallodapines investigated by the author.

In February 1982 I sent copies of Figures 1–3 (except Fig. 2f) presented in this paper to 17 heteropterists, including several mirid specialists, in order to better inform myself about the taxonomic status of this remarkable mirid from West Africa. As the male genitalia (Fig. 3) indicate, it clearly belongs in the Phylinae, Hallodapini. Because I am not a mirid specialist, I wanted to be sure whether the species was already described before preparing a short note on its exceptional cephalic modifications, which give the illusion of the head of an ant. Of the several replies to my question, two colleagues (Dr. Akingbohungbe, Nigeria, and Dr. Linnavuori, Finland) informed me that the animal in question already had a name. It was described by Linnavuori (1974) as *Leaina belua* new genus and species (Hallodapinae[1]) based on material from the Ivory Coast. Although Linnavuori mentioned the remarkably antlike habitus in his formal description of the genus and species, the phenomenon remained somewhat hidden in his taxonomic treatment of many other new taxa. Therefore, it may be of general interest to focus special attention on it in this commemorative issue at the occasion of Dr. Froeschner's seventieth birthday. I will not detail the vast literature on "ant mimics" in Heteroptera. My only hope is that this note will stimulate biologists to make careful observations on the biology of this and other ant like forms in Africa and elsewhere and to set up experiments for analyzing the functional significance, if any, of myrmecomorphy.

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[1] Linnavuori followed Wagner (1970) in giving the hallodapines subfamily rank. I agree with Schuh (1974:292) that this position "has little merit, because it is based only on the superficial uniqueness of the group." It would moreover cause the family to be split up in an endless mass of subfamilies if this procedure were be followed consistently.

STRUCTURAL PECULIARITIES OF *Leaina belua* AND SOME OTHER PHYLINAE

The single male that came to my disposal originated from the Ivory Coast, Katiola savanne, 54 km N of Bouaké, 26.XI.1980. It was caught in a pit-fall trap (KAS 2) during a large-scale sampling survey for studying residual effects of insecticides on invertebrates after tsetse fly control by aerial spraying. This program was supervised by the Department of Toxicology (Wageningen). Mr. J. Everts, coordinator of the program, made part of the samples which were separated in Africa by insect order, available to us. It is not surprising that the mirid bug was stored in a vial with otherwise only small Hymenoptera. Dr. Akingbohungbe informed me that he has in his collection the same species, collected in Nigeria, Ilora, in the derived savanna area of Oyo state (2 males in Malaise trap, 19.VIII.1974, J. T. Medler collector).

After the single male was compared with the description of *L. belua,* the length of the labium appeared to be different. According to Linnavuori (1974), the rostrum should extend to the metasternum, whereas in our specimen it does not surpass the first coxae (Fig. 1). This latter condition, however, holds also for the holotype male of *L. belua,* which I was able to study. Small differences between Linnavuori's and my figures of genitalia may be due to different angles of viewing, so I consider the male at hand conspecific with *L. belua.*

The most striking myrmecomorphic traits of this species are found on the head. The general facies of the insect in dorsal view (Fig. 2a) is shared by many other antlike Miridae: eyes removed from pronotal margin, convex connection of head with anteriorly narrowed pronotum, wing margin sinuate, white fascia medially on the brownish corium, and abdomen globular and constricted at base. Sex-related brachyptery is another phenomenon often associated with myrmecomorphy; the wings of the female of *L. belua* are said to be strongly reduced. The dramatic deviations from the generalized mirid head (Fig. 1a) become apparent in frontal (Fig. 2d) and lateral views (Figs. l, 2b, c). The head is diagnosed as follows: proportionally large, elongate with narrow neck; narrow ellipsoid eyes; antennal sockets situated between anterior edges of eyes; ventral surface of head strongly excavated laterally, the buccular region forming a thin keel-like vertical plate, this large foliaceous buccular expansion tightly encompassing the first labial segment. The unique cephalic structure involves the enlargement and elongation of the genae anteriad, extending sharply triangularly beyond apex of the partly concealed clypeus. The external margin of the gena is formed by a sharp horizontal carina starting from the upper anterior edge of the eye. These dark-colored genal transformations are reminiscent of orthopterous mandibles, at least to an entomologist, particularly in lateral view. As a consequence of these outgrowths and the keel-like projection of the gular region, the limits between lora and buccula are indistinct; remnants of them are visible underneath the genae (arrow in Fig. 2c). The antlike shape of the head is further enhanced by the long, laterally flattened, scapus-like second antennal segment, which is bent elbow-like with respect to the remaining slender segments (Fig. 1). It is not known whether the antennae are kept folded in living specimens. Note further that the labrum and labium are short and inconspicuous.

In any larger treatment of the diverse family Miridae the term myrmecomorphic

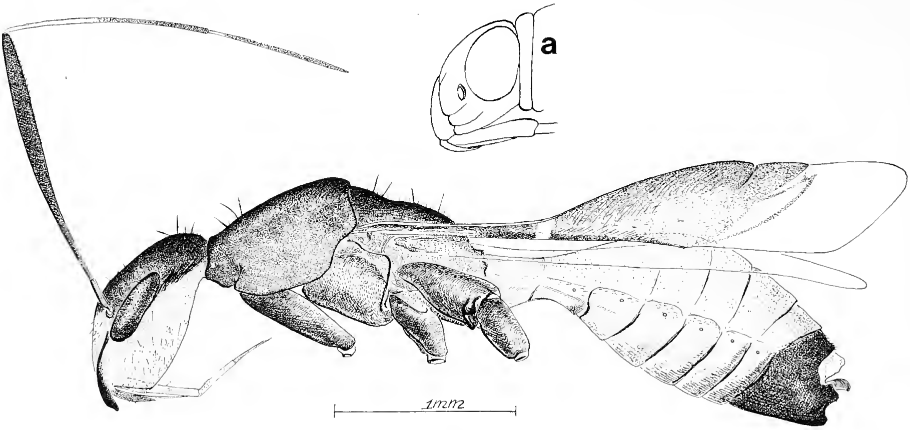

Fig. 1. *Leaina belua.* Left lateral view of male, legs omitted. a, lateral view of generalized mirid head.

is encountered repeatedly (e.g., Slater and Baranowski, 1978; Schuh, 1974; Wagner and Weber, 1964; Kullenberg, 1946). Particularly, the Phylinae of the Old World tropics as illustrated in the revisions of Schuh (1974, 1984) and Orthotylinae and Mirinae in the Neotropics show a multitude of morphological adaptations producing antlike appearance not equalled in any other family. From such analyses it also becomes clear that antlike mirids have evolved independently many times. What struck me most in reading the work of Schuh was that a kind of cephalic type described here for a hallodapine seems to reach a pinnacle in two other tribes of the Phylinae. Schuh (1974:258–259) stated: "In certain undescribed genera in the Pilophorini and Leucophoropterini the gula [*sic*] is carinate below the eye and gives the appearance of mandibles when viewed anteriorly. All of these structural characteristics have evolved more than once and are therefore indicative of the extreme adaptablility of the Miridae to ant-mimic selection." However, on page 305 in the same work and dealing with the Leucophoropterini, Schuh speaks of the carinate gena forming a broad ridge below the eye, indicating a lapsus in the statement above.

Another example in the Phylinae where structures have evolved that remind us of orthopteroid mandibles should be noted. Mr. Dolling wrote me after he had compared my illustrations of the then unknown hallodapine with material in the BM collections: "In many Hallodapini the labrum is very broad in the vertical plane." I sorted, in the Tervuren collections, a series of unidentified species from Africa that reveals this vertical dilation of the labrum in various degrees. In the most extreme case I have seen, the labrum appears like a thin blade through lateral compression (Fig. 2f, f′). Although unpaired, this development could have the advantage over the paired outgrowths in *L. belua* that it is movable and supposedly more efficient if it indeed functions for advertisement. In contrast to *L. belua,* all these bugs with an enlarged labrum have a solid, long rostrum. An enlarged laterally flattened labrum occurs also in the New Guineaian genus *Gulacapsus* Schuh, Phylinae, Leucophoropterini (see Schuh, 1984:230), and in the African hallodapine genus *Skukuza* Schuh, 1984 (Fig. 62 in Odhiambo, 1959).

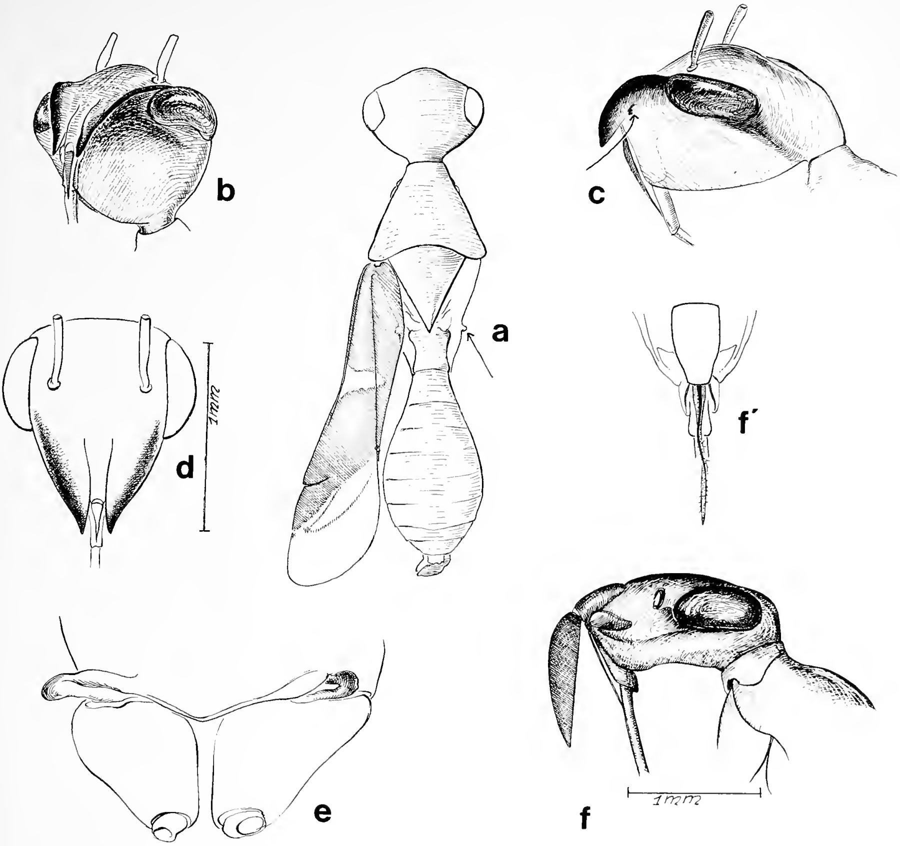

Fig. 2. a–e, *L. belua*, ♂; a, dorsal aspect; b–d, head viewed from different angles in order to show the mandibular-like projections of the genae; e, metathorax, ventral view, evaporatory area in front of metacoxa. f, lateral view of head and thorax of unidentified species (male) from Tanzania (Longido, Masai Distr., 1,500 m, 19.IV.1957, in Musée Royal de l'Afrique Centrale, Tervuren, Belgium); note the enlargment of the labrum, which is shown in dorsal view in f′.

DISCUSSION

The biological significance of antlike habitus in many Miridae is a matter of speculation. In the absence of experimental evidence to confirm a selective advantage for the "ant mimics," the only valid neutral term for the phenomenon, as it manifests itself to us, would be myrmecomorphy and the respective bugs myrmecomorphic. The suggestion that the mistletoe mirid *Phoradendrepulus myrmecomorphus,* described recently by Polhemus and Polhemus (1985), in the subfamily Phylinae but not assigned tribe, is myrmecophilic because it is invariably taken in the company of *Crematogaster* sp., is premature.

It may be relevant to focus here on the lengthy discussion of this subject by Kullenberg (1946:10–16, 481–491) in his classic work on the biology of Northern

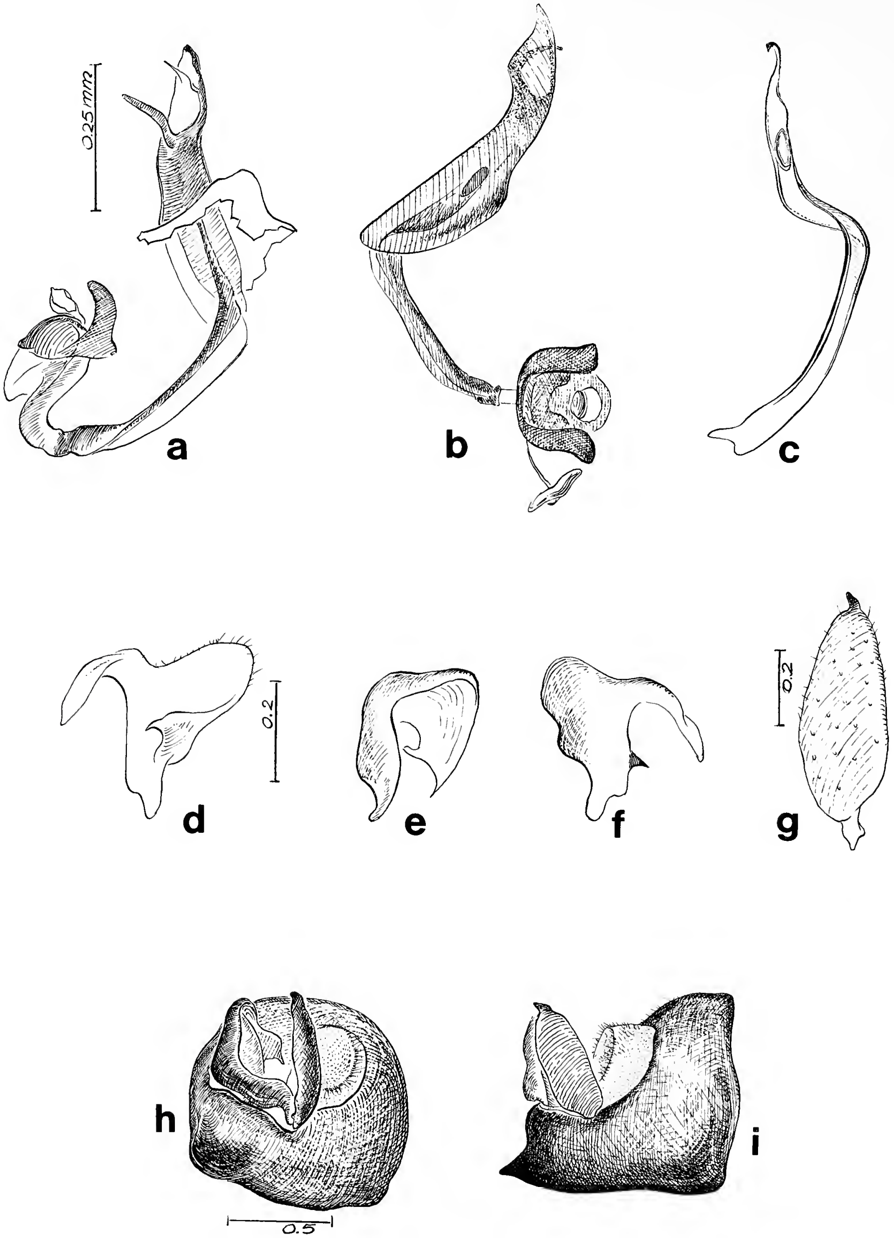

Fig. 3. Male genitalia of *L. belua.* a, b, phallus and phallotheca; c, vesica; d–f, different views of left paramere; g, right paramere; h, i, genital capsule, phallus removed; h, oblique dorsal view; i, right lateral view.

European Miridae. The German language is possibly the reason that no reference is made to it in English literature dealing with the topic of ant mimicry. In Northern Europe, the ground-dwelling thermophilous *Myrmecoris gracilis* and *Systellonotus triguttatus* are the most striking myrmecomorphic species of the 90 species studied by Kullenberg. It cannot be denied that the uniformly brown micropterous specimens look superfically very antlike (Fig. 4a, b). *Myrmecoris gracilis* belongs in the Mirinae, Pithanini, and nearly all its attributes have been involved in changes of the basic body plan. Whereas "ant mimics" of other subfamilies show extreme modifications of the pronotum, sometimes much more excessively than appears from Figure 1, it is the mesothorax in *Myrmecoris* that produces the nearly hour-glass shape of the thorax (Fig. 4a, a′; note the displacement of the wing bases far back from the pronotum). I was further surprised to find that the labrum is enlarged in the vertical plane (Fig. 4a′), thus showing a tendency towards "false-mandible formation" ultimately realized in the African mirid illustrated in Figure 2f.

What kind of biological evidence do we have that might support our intuitive feeling of functional ant mimicry of these two European mirid bugs? I summarize here the observations and interpretations of Kullenberg (1946). Of all the species studied, *M. gracilis* and *S. triguttatus* have the strongest need for animal food[2], which consists in the field predominantly of aphids; they certainly are not myrmecophagous as was suggested in older literature. The bugs show no special preference for aphid colonies that are visited by ants. If ants encounter the bugs in aphid colonies, the bugs will invariably be chased away; in insectaries they were always killed by the ants. The two color forms in *M. gracilis,* which are said to each mimic a different species of *Formica* (Reuter, 1879; Wagner and Weber, 1964:78), are considered by Kullenberg to be of no significance regarding protection against ants. The behavior of the bugs is very agile with rapid motions of the antennae, which are not bent in the ant-like fashion. Kullenberg preferred to restrict the term myrmecomorphy (his "Myrmecoidie") exclusively to shape and color and not to behavior, because there are nonmyrmecomorphic mirids that show ant-like behavior (he did not present examples). The protecting role of the antlike habitus against predators (birds, spiders, or insects) was greatly doubted by Kullenberg, but he did not provide evidence to the contrary. In the field he had not observed any predator acting on the myrmecomorphic bugs and he had not carried out experiments with potential predators. The fact that "normal" looking mirids became alert when an ant was approaching but behaved indifferently to antlike bugs led Kullenberg to suggest that something other than optical stimuli (e.g., substrate vibration, chemical stimuli) was more important to the insects ability to discriminate between ants and harmless antlike insects. On the other hand, the same author referred to experiments of Palmgren (1937) in which it was shown that five insect-eating birds avoided eating ants and also refused one antlike spider. One individual bird later learned to discriminate between ants and spiders and accepted the latter readily. The final conclusion of

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[2] It is generally assumed (e.g., Schuh, 1974) that most if not all clearly ant-looking mirids are mainly carnivorous. Interestingly, the second Pithanini in NW Europe, *Pithanus maerkeli* H.-S., which is much less antlike than *M. gracilis,* is 100 percent phytophagous.

Kullenberg (1946) was that there was no valid argument for the selective advantage of antlike form in the Miridae; he declared the biological meaning of myrmecomorphy as completely open for testing; one feels from his reasoning that he considered the antlike facies to have been evolved by process of chance.

Still, I think that any heteropterist who is impressed by the multitude of antlike forms paralleled in various families, implicitly feels that such bugs must have or have had great selective advantages because of their antlike appearance. We had to wait about 40 years after the comments of Kullenberg and other authors before more meaningful data with respect to the selective value of ant mimicry in bugs became available, albeit not yet in Miridae. The recent data are assembled from detailed observations on, and experiments with, two species of *Hyalymenus* in association with large complexes of ants in Brazil (Oliveira, 1985). The situation in these Alydidae is different from Miridae in two respects. Only the larvae are myrmecomorphic and diurnal; the adults are not antlike and they are mainly nocturnal. Both larvae and adults feed in aggregations on reproductive parts of plants. One of the alydid species studied lives on plants belonging to several families, including composites; the other species consumes sap only from solanaceous flowers and fruits. Many ant species forage on the same upper parts of these weeds, mostly feeding from honeydew-producing homopterans. The myrmecomorphy of the bugs is enhanced by antlike behavior, notably rapid zig-zag locomotion, constantly agitated antennae, and up and down movement of the abdomen. Oliveira is convinced that the larvae of the bugs under investigation act as mimics of certain ants and his data seem indicative of such relations. He suggests that the color and size changes through different larval instars "allow the immature bugs to mimic, during their development, different castes of a given ant model, as well as differently sized and coloured ant species." In one area a particular fourth instar color morph of one of the two bug species is considered as a species-specific mimic of one ant species. The last instars of the same alydid species are dimorphic, black or yellow. The proportions of these are different in two areas, matching the significant differences between color patterns of both ant faunas. The behavioral interactions between *Hyalymenus* larvae and the supposed ant models in the field, as described by Oliveira, are suggestive of a more or less tolerant attitude between both partners, whereas other ants evoked conspicuous avoidance reactions. Interesting as these results are, counts of the proportions of morphs between populations of the supposed mimics in relation to ant composition have to be extended over longer periods of time. The survey made to assess the stated correlation was apparently done only once, considering the rather low number of bug larvae counted. To test the hypothesis of Oliveira that larvae of *Hyalymenus* gain Batesian or Müllerian protection by resembling available ant models of different Müllerian complexes needs further extensive research. The only experiment with potential non-ant predators of the bugs was done with a praying mantid occurring in the same habitat. In captivity, the mantid attacked adult *Hyalymenus* but avoided encounters with the larvae, as well as with ants. These observations, however, are based on a few trials with only one mantid individual.

Returning to the myrmecomorphic mirids, one would be very lucky if some basic data as for alydids were available. That even weakly myrmecomorphic mirids have some profit from this resemblance may be assumed, but in order to prove it, the advantage must in some way be measurable. This would be very difficult or even impossible if the original biotic circumstances changed in such a way that the model-mimic system no longer exists. One of the characters shared by many unrelated groups of often ground-dwelling mirids, whether they are weakly or strongly myrmecomorphic, is the wing pattern: brownish with a contrasting white hemelytral fascia. Since in other families this pattern often occurs with other myrmecomorphic traits (e.g., in Lygaeidae, Slater, 1982; in Saldidae, 3 times independently, Cobben, in press), it might be possible that the wing design, on its own or combined with behavior modification, grants some initial protection against certain predators. As is apparent from the observations of Kullenberg (1946), gaining insight into the selective value of a reasonably well-developed ant-mimicry system in the Miridae will be much more difficult than in the Alydidae. It would be more feasible to address the problem of mimicry in striking examples such as *Leaina belua* or other African hallodapines. If such species indeed appear entirely dependent on living aphids, they would be the direct competitors of aphid-milking ants[3]. It seems inconceivable that *L. belua* with its extraordinary cephalic adaptations and short rostrum (Fig. 1) could interfere with trophallaxis among ants, but then results of modern research on mimicry sometimes have exceeded our wildest expectations. Chemical interference with ants also is not *a priori* excluded. Typical ant-mimetic mirids have tuberculate outlets of the metathoracic glands (Figs. 2e, 4a, arrow), whereas a quick survey of my collection of Dutch mirids showed that the evaporative areas in nonmimics do not project from the thoracic sides[4]. Field observations and experiments on such aspects have to be done where such peculiar mirids live in Africa or other tropical regions. I hope that such studies can be undertaken before drastic environmental changes make them impossible.

There is another reason why heteropterists should study hallodapines. During a field study in Ethiopia in 1969, I collected *Hallodapus albofasciatus* (Motschulsky) everywhere in the environment of Jimma (Kaffa Prov.). This species (about 3 mm long) is ground living, preferring fallow land and has a very wide distribution in the Old World tropics (Schuh, 1974, 1984). Although a typical hallodapine with a transverse white fascia on castaneous-brown wings, it is not particularly antlike. About 80–90% of the females I collected were brachypterous, the hind wings reduced to stubs.

From a rough inspection of testis squash preparations made in Jimma, I concluded that this species revealed a karyotype of $2n = 4$. Last larval instars and adults were

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[3] In this connection it is relevant to quote an important comment of A. Akingbohungbe (pers. comm.): "Rather amazingly, several isometopines of the tribe Myiommini from Asia and tropical America show varying degrees of modification of the facial plates, not too far removed from being a progression towards development of 'false mandibles.' For example, in *Totta* Ghauri from India, the tylus projects prominently forward over the base of the rostrum very much like lateral facial plates (i.e., genae, bucculae) that become modified and projected forwards (see Henry, 1980, Proc. Entomol. Soc. Wash. 82:178–194). As isometopines are now commonly associated with scales as predators, and scales are often tended by ants, your hypothesis on functional false mandibles may probably apply to them too!"

[4] However, A. Akingbohungbe and R. T. Schuh inform me that protruding outgrowths of the scent glands do not occur in all ant-like mirids, whereas tuberculate outlets are also present in some non-myrmecomorphic taxa such as *Fingulus, Angerianus,* and *Stethoconus.*

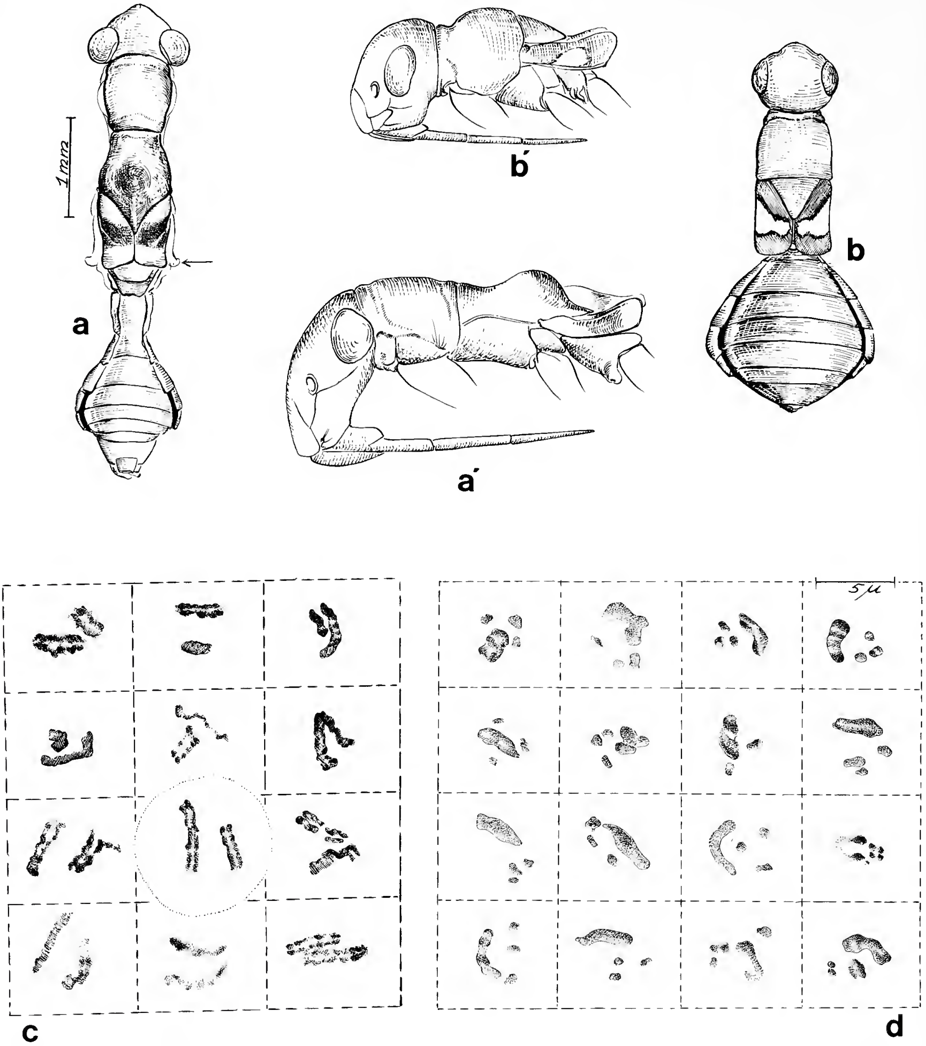

Fig. 4. a, a′, *Myrmecoris gracilis,* dorsal and lateral views, respectively; b, b′, *Systellonotus triguttatus,* idem. c, d, chromosome numbers in *Hallodapus albofasciatus* (c) and *Systellonotus alpinus* (d) testes, metaphase I.

transferred to Wageningen and kept alive for several weeks on a diet of wounded but still moving *Drosophila* files. Again the chromosome number of several males was investigated, which consistently appeared to be two, very rarely three, haploid (Fig. 4c). This is the lowest number known in Heteroptera. Cytological data are now available for more than 900 species of Heteroptera in all families except a few (review in Ushima, 1979, and later references). There is only one other species known with 2n = 4, *viz.,* an unidentified *Lethocerus* sp. from Michigan. Since some other *Leth-*

ocerus spp. have numbers up to 30, it has been suggested (Chickering and Bacorn, 1933; Ueshima, 1979) that the x and y have both been translocated to one pair of autosomes and that fusion has occurred between pairs of autosomes. Although fusion of holocentric chromosomes is considered a rare phenomenon in comparison with fragmentation (Ueshima, 1979), the situation of $2n = 4$ in *H. albofasciatus* cannot be explained other than by fusion. The known diploid range in Miridae (73 genera, 167 species studied) is 14 to 80; 80 is the highest number in the Heteroptera. Two species of Hallodapini, one from Japan and the other from USA investigated by other authors, have $2n = 26$ and 34, respectively. The modal number of the subfamily, to which this tribe belongs, appears to be $30 + xy$ (17 genera, 37 species; Ueshima 1979). Another myrmecomorphic hallodapine from Switzerland (*Systellonotus alpinus* Frey), which I have examined, also deviated from this general pattern because it possesses 8 chromosomes in the diploid state (Fig. 4d). If chromosome reduction would appear to be more widespread in the hallodapines, further extensive studies would be of great importance to cytologists interested in modes of chromosome change.

It is difficult to see any direct connection between the karyological phenomenon mentioned and myrmecomorphy. There might, however, be an indirect relation, as chromosome reduction would appear to be associated with the type of sexual dimorphism commonly found in myrmecomorphic Phylinae: males always macropterous, females usually brachypterous or micropterous. I am not aware of any such correlation in other insect orders. It is unfortunate that Microphysidae, which show a consistent striking sexual dimorphism in wing development, belong to one of the very few heteropterous families of which karyological data are entirely unknown.

ACKNOWLEDGMENTS

Thanks are due to J. Everts, Department of Toxicology, Wageningen, for allowing me to examine the mirid from the Ivory Coast; to R. Linnavuori for sending type material of *Leaina belua;* to A. Akingbohungbe, W. R. Dolling, and R. T. Schuh for helpful comments; and A. G. Wheeler and T. J. Henry for corrections of the English text. Figure 4C is based on photographs taken by B. Kiauta, Utrecht University.

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J. New York Entomol. Soc. 94(2):205–216, 1986

NEOTROPICAL MIRIDAE, CCLXV: DESCRIPTIONS OF NEW TAXA AND TAXONOMIC NOTES (HETEROPTERA)

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Abstract.—The present paper contains descriptions and habitus illustrations of the following new Miridae: *Araucanomiris,* new genus (type species *Adelphocoris chilensis* Carvalho and Maldonado); *Froeschneriella,* new genus, *F. elsiae,* new species (Ecuador); *Phytocoris minensis,* new species (Brazil); *Proba froeschneri,* new species (Mexico); *Paraguayna,* new genus, (type species *Neofurius paraguayensis* Carvalho and Drake); *Ilnacora arnaudi,* new species (Mexico). *Eroticoris albiceps* Lethierry is transferred to *Neofurius* Distant, new combination. A lectoctype is designated for *Aspidobothrus latipennis* Reuter.

In studying specimens of Miridae sent to me for identification by Dr. P. H. Arnaud, Jr., California Academy of Sciences, I discovered a number of undescribed genera and species of Miridae. My findings are presented in this paper, which is specially written to commemorate the seventieth birthday of Dr. Richard C. Froeschner, curator of Hemiptera, National Museum of Natural History, Washington, D.C.

Dr. Froeschner and I were companions at Iowa State College (presently Iowa State University of Science and Technology), Ames, Iowa. I had the privilege to enjoy his fellowship and our mutual friendship which extended to our wives and daughters. We used to frequent the home of Dr. Harry H. Knight and his wife Jessie to listen to music and watch television. During this period we also became friends with Drs. Carl J. Drake, Halbert M. Harris, and Leonard A. Kelton, James A. Slater, Joseph C. Schaffner.

It was during these years that I grew to admire Dick for his companionship and close collaboration. My admiration also extended to his wife, Elsie, not only because she was an excellent mother and clever wife, but also because of her excellent entomological illustrations. Our affection was so strong that during a trip to the Western United States, we stopped at Boseman, Montana, where Dick was Professor of Biology at the University of Montana. My wife Milza, and I were very pleased when we learned that he was soon to take on a new position as curator of Hemptera at the United States National Museum of Natural History. During his years at the Museum, we had several opportunities to visit the Froeschners in Washington, D.C. and to correspond. I am one of the many people who has benefited very much from his friendly cooperation. It is then with great pleasure that I take this opportunity to acknowlege these many years of collaboration and pay modest honor to an excellent friend.

All measurements are in millimeters.

SUBFAMILY MIRINAE

Tribe Mirini

Araucanomiris, new genus

Diagnosis. This genus belongs to the group of mirids with a distinctly punctate and noticeably rugose scutellum, and the cuneus much longer than wide at base. It presents the general facies of *Adelphocoris* Reuter, 1896, by the strongly punctate pronotum and by the noticeably long cuneus, as well as the long rostrum.

Description. Body noticeably elongate, covered by dense semierect pubescence.

Head slightly inclined, vertex weakly marginate, frons prominent, striate, eyes rounded, contiguous with collar, antenna cylindrical, with short hairs, segment I slightly shorter than width of head, segment II about three times longer than first, very slightly thickened toward apex, clypeus prominent, rounded, lorum also prominent, eyes seen from side reaching gula, rostrum reaching middle coxae, segment I attaining midpoint of medially sulcate prosternum xyphus.

Pronotum strongly punctate, collar wide, calli flat, reaching sides of disc, hind margin straight; mesoscutum largely exposed, scutellum prominent, noticeably rugose.

Hemelytra with sides parallel, embolium explanate, narrow, cuneus noticeably longer than wide at base, narrowed toward apex, membrane biareolate, cells elongate.

Underside of body with propleura narrowed posteriorly, mesosternum large, ostiolar peritreme small, legs long and slender.

Type species. Adelphocoris chilensis Carvalho and Maldonado, 1973.

Froeschneriella, new genus

Diagnosis. This genus approaches *Neurocolpus* Reuter, 1876, in the general facies but lacks scalelike setae on first antennal segment.

Description. Body elongate, densely covered by long erect hairs, intermixed with woolly adpressed pubescence covering a silvery pruinosity distinctly visible on the hemelytra, the base of some hairs showing minuscule grains especially on disc of pronotum and scutellum, surface without punctures.

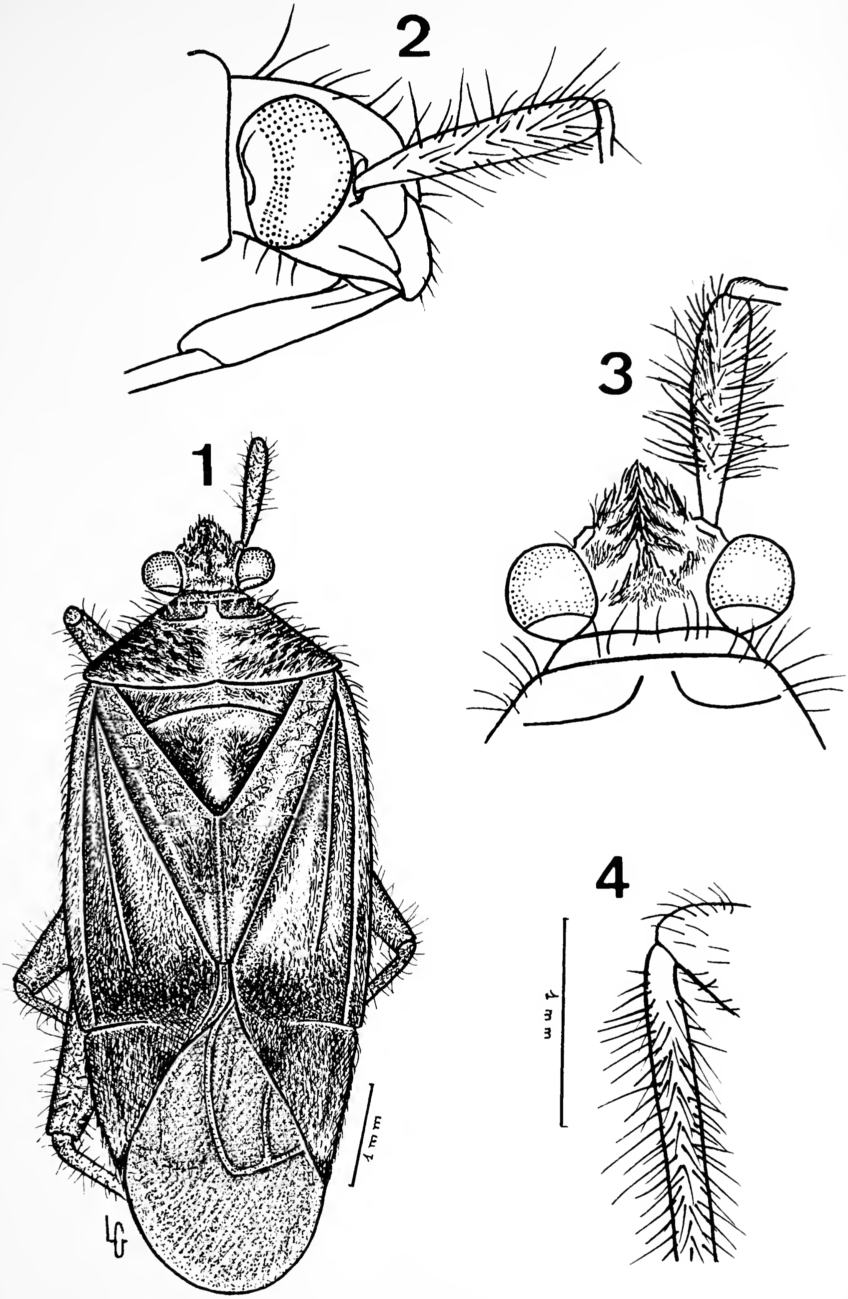
Head semihorizontal, vertex depressed at middle, a short neck present, frons striated and prominent, eyes slightly removed from collar by a distance approximately equal to diameter of second antennal segment, hind margin smooth, inclined forward; antennae with segment I noticeably incrassate toward apex, covered by very long setae, about as long as or longer than thickeness of segment, segment II very slender, cylindrical, with very short hairs (segments III and IV mutilated); rostrum very long, reaching beyond hind coxae (about middle of abdomen).

Pronotum inclined and narrowed anteriorly collar wide, calli wide and flat, middle portion of disc depressed longitudinally, hind margin straight at middle, curved inward before humeral angles; mesoscutum exposed, scutellum very prominent.

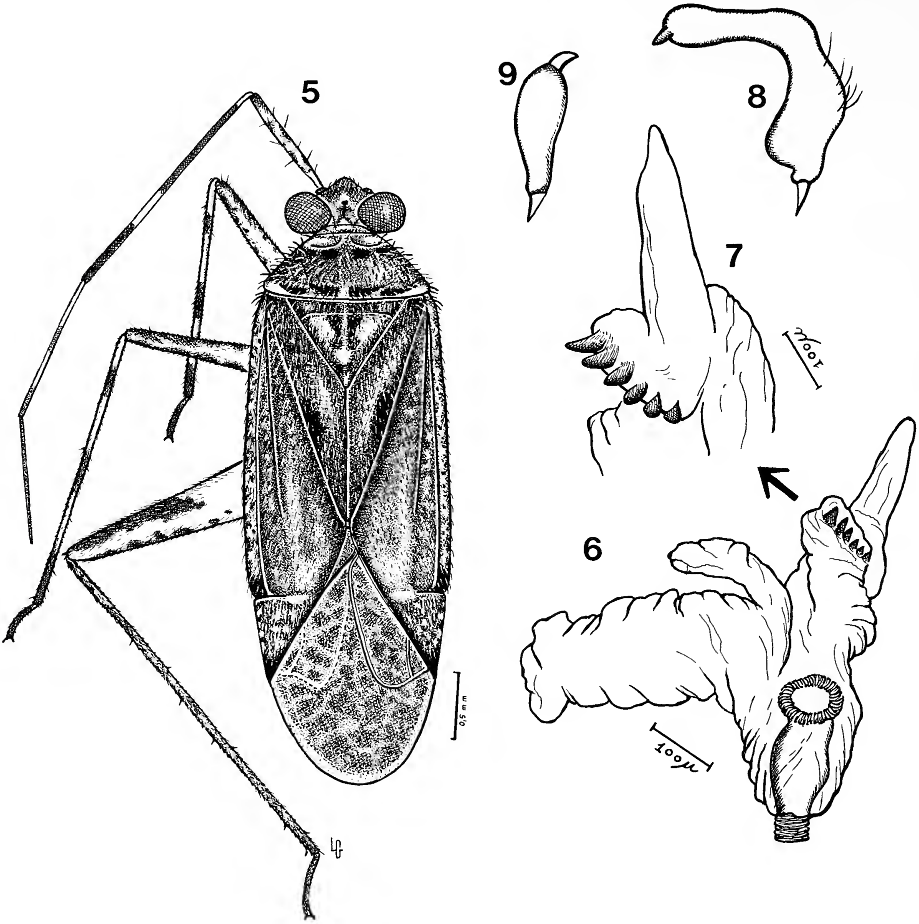
Hemelytra with claval vein prominent, embolium wide, cuneus about twice as long as wide at base, membrane biareolate.

Legs densely pilose, tibiae with numerous setae about as long as or longer than their thickness.

Type species. Froeschneriella elsieae, new species.



Figs. 1–4. *Froeschneriella elsiae*. 1. Female, holotype. 2. Side view of head. 3. Head and first antenna seen from above. 4. Basal portion of hind tibia.



Figs. 5–9. *Phytocoris minensis.* 5. Habitus. 6. Vesica of aedeagus. 7. Sclerotized comb of vesica. 8. Left paramere. 9. Right paramere.

Etymology. The name is given in honor to my colleague Richard C. Froeschner in recognition of his work on the Hemiptera.

Froeschneriella elsiae, new species
Figs. 1–4

Diagnosis. Characterized by its color and dimensions.

Description. Female: Length 7.2, width 2.8. *Head:* Length 0.6, width 1.2, vertex 0.50. *Antenna:* Segment I, length 1.1; II, 2.8; III and IV mutilated. *Pronotum:* Length 1.0, width at base 2.4. *Cuneus:* Length 1.20, width at base 0.80 (holotype).

General coloration brown, intermixed with dark brown to black areas; head pale yellow with an X-like dark spot on vertex, striae of frons and eyes brown, neck pale, antenna with segment I pale and a few dark grains at base of setae, segment II brown with apical third dark, segment III with base pale.

Pronotum brown with some darker grains at bases of hairs, humeral angles with dark spots and tufts of hairs on both sides of hind margin and middle of scutellum; longitudinal middle portion of disc paler.

Hemelytra brown with some irregular darker areas, apical portion of clavus paler, transverse distal fascia of corium and embolium dark brown, cuneus brown with a dark spot over paracuneus, membrane fuscous, covered by silvery pruinosity.

Underside of body with a mixture of brown and pale yellow, coxae and femora brown with numerous small pale spots, hind femora with a pale band at middle, tibiae with four dark rings, tarsi with apical segment black.

Male: Unknown.

Holotype. ♀, ECUADOR, 2 mi N of Santa Rosa, El Oro, 10 m, 1.24.55, E. I. Schlinger and E. S. Ross; deposited in the California Academy of Sciences, San Francisco.

Etymology. The specific name is dedicated to Elsie Froeschner in recognition of her illustrative work on numerous insects, including many hemipteran species.

Phytocoris minensis, new species

Figs. 5–9

Diagnosis. Characterized by the color of scutellum and by the morphology of the male genitalia, by which characters it can be distinguished from *Phytocoris bergrothi,* Reuter, 1892.

Description. Male: Length 4.8, width 1.6. *Head:* Length 0.3, width 0.9, vertex 0.20. *Antenna:* Segment I, length 0.8; II, 2.0; III, 1.2; IV, 0.9. *Pronotum:* Length 0.5, width at base 1.2. *Cuneus:* Length 0.70, width at base 0.40 (holotype).

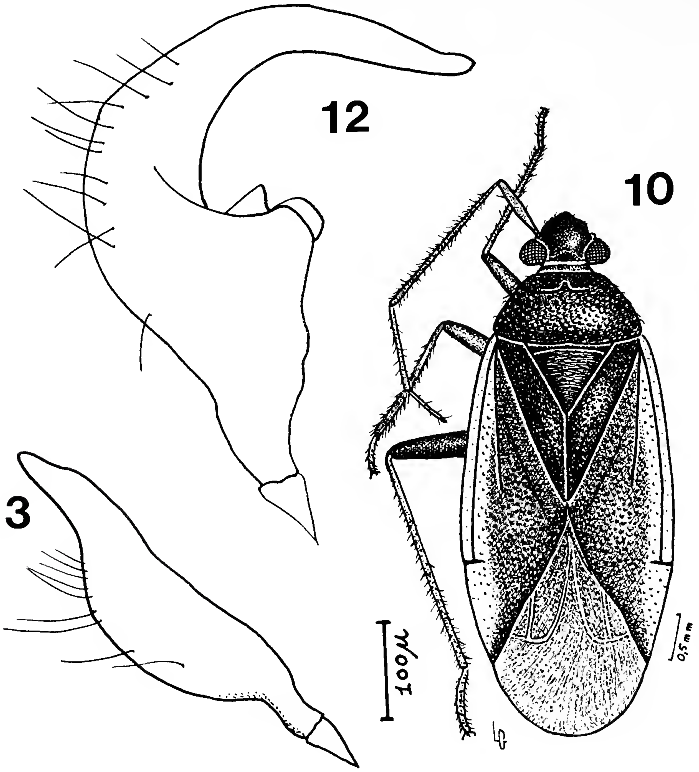
General coloration brown with pale yellow, black and green areas; head brown with pale spots on frons and margin of eye, neck whitish with two brown longitudinal fasciae as seen from above, antenna with segment I pale, speckled with brown, segment II black with a basal and a median pale ring, segment II black, white basally, segment IV fuscous.

Pronotum brown, area of calli and hind margin of disc (in some specimens with only three elongate spots) pale, two spots behind calli (at each side) and a submarginal transverse fascia (in some specimens seen as tufts of hairs) black; mesoscutum brown with two pale spots laterally, scutellum green with a median longitudinal fascia (divided or not by a pale line) branched subapically into two black spots, apex pale.

Hemelytra brown, mottled with pale, light brown on endocorium, darker along veins, embolium with alternate pale and brown spots, cuneus brown, speckled with pale, spot on paracuneus, basal third of inner margin and apex black; membrane pale, marmorate with brown, smaller vein with a longitudinal or oblique dark fascia.

Underside of body brown, gula, xyphus of prosternum, coxae, coxal clefts and ostiolar peritreme whitish, legs pale speckled with brown, hind femora dark apically, tibiae with an apical and median dark rings (sometimes also a basal one).

Body covered by long erect setae (especially on sides of calli and on collar) and stiff bristles, smooth, scutellum noticeably prominent on apical third, eyes very large, occupying most of lateral portion of head, segment I of antenna with erect setae, segment II with very short hairs, rostrum reaching abdominal segment VIII.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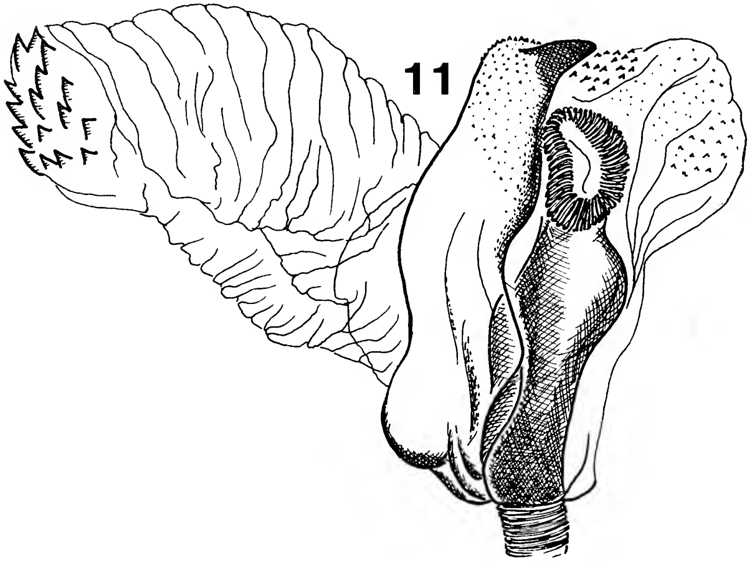

11

Genitalia: Vesica of aedeagus (Figs. 6, 7) membranous, with a characteristic structure at one of the lobes, consisting of six sclerotized teeth and a pointed prolongation. Left paramere (Fig. 8) curved, with a few setae dorsally and an acute apex. Right paramere (Fig. 9) small, ended by a sclerotized lobe.

Female: Similar to male in coloration and general aspect, vertex 0.36, cuneus length 0.80, width at base 0.50, rostrum reaching base of ovipositor.

Holotype. ♂, BRAZIL, **Minas Gerais,** Vicosa, 13.X–15.IX.82, Fiuza and Martins; deposited in the collection of the National Museum, Rio de Janeiro.

Paratypes. 3♂♂ and 1♀, same data as holotype; deposited in the collections of the Department of Biology, Federal University of Vicosa, Minas Gerais, and the author.

Etymology. The specific name refers to the state of Minas Gerais where the specimens were collected.

Proba froeschneri, new species

Figs. 10–13

Diagnosis. Characterized by the color of the hemelytra, the long setae on the underside of the second femur, and the morphology of the male genitalia.

Description. Male: Length 6.2, width 2.6. *Head:* Length 0.4, width 1.2, vertex 0.52. *Antenna:* Segment I, length 0.6; II, 1.8; III, 1.0; IV, 0.6. *Pronotum:* Length 0.8, width at base 1.8. *Cuneus:* Length 1.10, width at base 0.60 (holotype).

General coloration dark brown to black with pale yellow areas; head black, hind margin of vertex pale, eyes brown, exocorium, embolium and outer portion of cuneus pale yellow, membrane fuscous, nervures darker. Underside of body dark brown, tibiae paler on apical portion, rostrum pale yellow.

Body practically glabrous (only a few very short hairs present on cuneus and embolium), punctate, scutellum rugose, membrane translucent, vertex marginate and slightly curved, eyes contiguous to pronotum, antenna with short setae (apical portion of segments II, III and IV with a few erect setae), rostrum long, reaching the hind coxae or slightly beyond, middle femur with a dense and long tuft of setae on underside, middle tibiae also with hairs, spines, and long setae, in both cases the length of setae is greater or equal than thickness of femur or tibia, calli and area between them without punctures.

Genitalia: Vesica of aedeagus (Fig. 11) with distal portion of seminal duct enlarged at middle, a spicular-like structure more sclerotized apically, and membranous lobes covered with small teeth, as seen in illustration. Left paramere (Fig. 12) curved, basal lobe prominent, followed by a small tooth-like structure, apical portion tapering distally and with numerous dorsal setae. Right paramere (Fig. 13) smaller, wider at middle, tapering distally, with a few dorsal setae.

Female: Similar to male in coloration and general aspect, with membrane slightly shorter. Length 5.6–6.0, vertex 0.60; setae ventrally on middle femur less numerous and shorter than in the male.

←

Figs. 10–13. *Proba froeschneri.* 10. Male, holotype. 11. Vesica of aedeagus. 12. Left paramere. 13. Right paramere.

Holotype. ♂, N.E. Citlaltepetl, Ver. (Veracruz), MEXICO, 6.27.64, elev. 11,000, L. W. Swan; deposited in the California Academy of Sciences, San Francisco.

Paratypes. 31♂♂ and 47♀♀, same data as for holotype, in the California Academy of Science and in the collections of the National Museum of Natural History, Washington, D.C., American Museum of Natural History, New York, British Museum (Natural History), London, and the author.

Etymology. The species is named after Dr. Richard C. Froeschner in recognition for his work on the Hemiptera and collaboration with other colleagues.

SUBFAMILY BRYOCORINAE

Tribe Eccritotarsini

Aspidobothrus latipennis Reuter

Aspidobothrys latipennis Reuter, 1907:34.
Aspidobothrus latipennis: Bergroth, 1922:16.
Aspidobothrus latipennis: Carvalho, 1957:91.

Discussion. This species was described by O. M. Reuter based on specimens from Brazil (Rio Grande do Sul, D. Stieglmayr; Sierra Geral, D. Hensel, Berlin Museum) and Paraguay (Villa Encovnacio Encarnacion, D. Schouteden). The syntype deposited at the Royal Institute of Natural Sciences of Brussels is hereby designated as lectotype.

Neofurius albiceps (Lethierry), **New Combination**

Fig. 14

Eroticoris albiceps Lethierry, 1881:5.
Hallodapus albiceps: Carvalho, 1958:168.

Discussion. The genus *Eroticoris* Douglas and Scott, 1865, was considered by Carvalho (1958) to be a synonym of *Hallodapus* Fieber, 1858, and as a consequence, species previously placed in *Eroticoris* were transferred to *Hallodapus.* Lethierry's species *albiceps,* described from the Island of Guadeloupe, was one of the species treated under Fieber's genus. Schuh (1974:92) recorded in his work: "A single species (*Hallodapus*) has been recorded from the New World (Carvalho, 1958); it is, however, not a species of *Hallodapus,* but belongs to the Bryocorinae, as I have confirmed by examination of the holotype [*sic*] of *Eroticoris albiceps* Lethierry in the Brussels Museum. *Eroticoris* is a junior synonym of *Hallodapus* and therefore *albiceps* will have to be placed in another existing genus or in a new genus. This action, however, will have to await study of *albiceps* by a specialist of the Bryocorinae." I have borrowed syntypes of *albiceps* from the Brussels Museum and find that it actually belongs in the genus *Neofurius* Distant, the species being recognizable by its coloration.

Diagnosis. Lectotype female: Length 4.6, width 1.4. *Head:* Length 0.3, width 0.6, vertex 0.42. *Antenna:* Segment I, length 0.6; II, 1.0; III, 0.6; IV, 0.6. *Pronotum:* Length 0.8, width at base 1.2. *Cuneus:* Length 0.80, width at base 0.50.

General coloration pale yellow to light lutescent with black areas; antennal segments II–IV and scutellum black, base of membrane fuscous.

Body with very fine erect hairs becoming more dense on embolar margins, rostrum reaching the middle coxae, portion anterior to calli wide, tibiae with fine hairs.

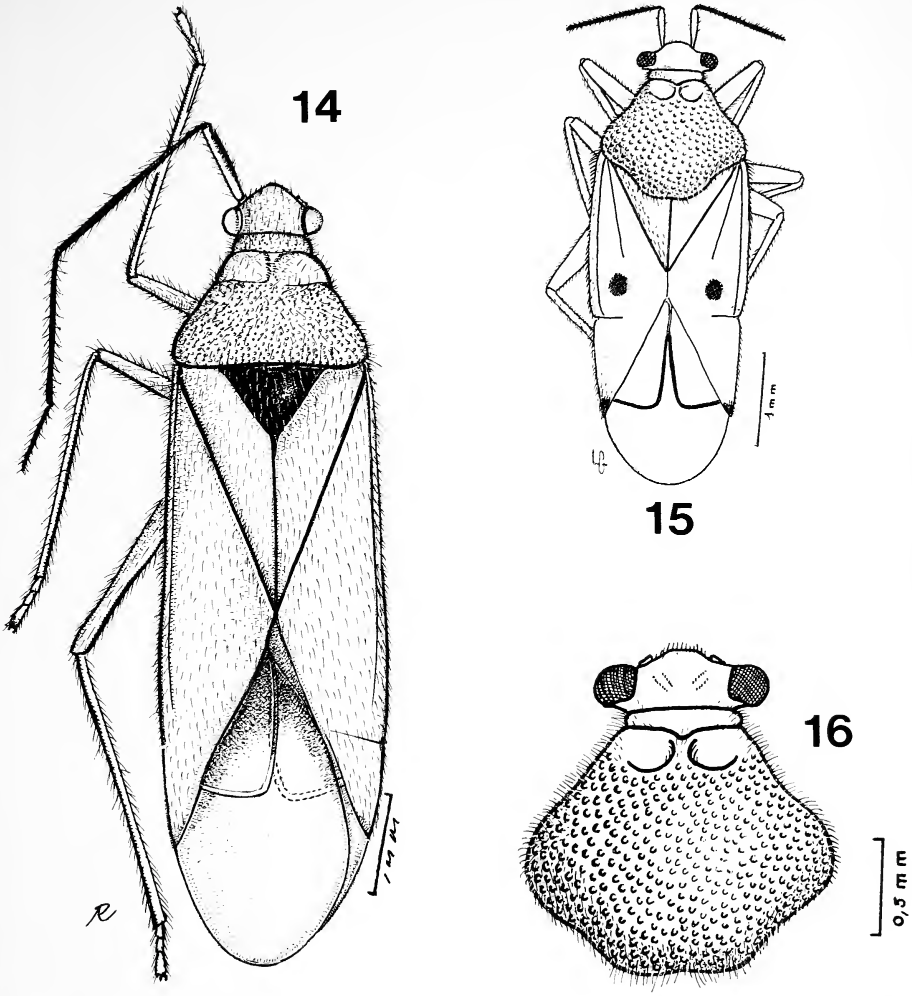


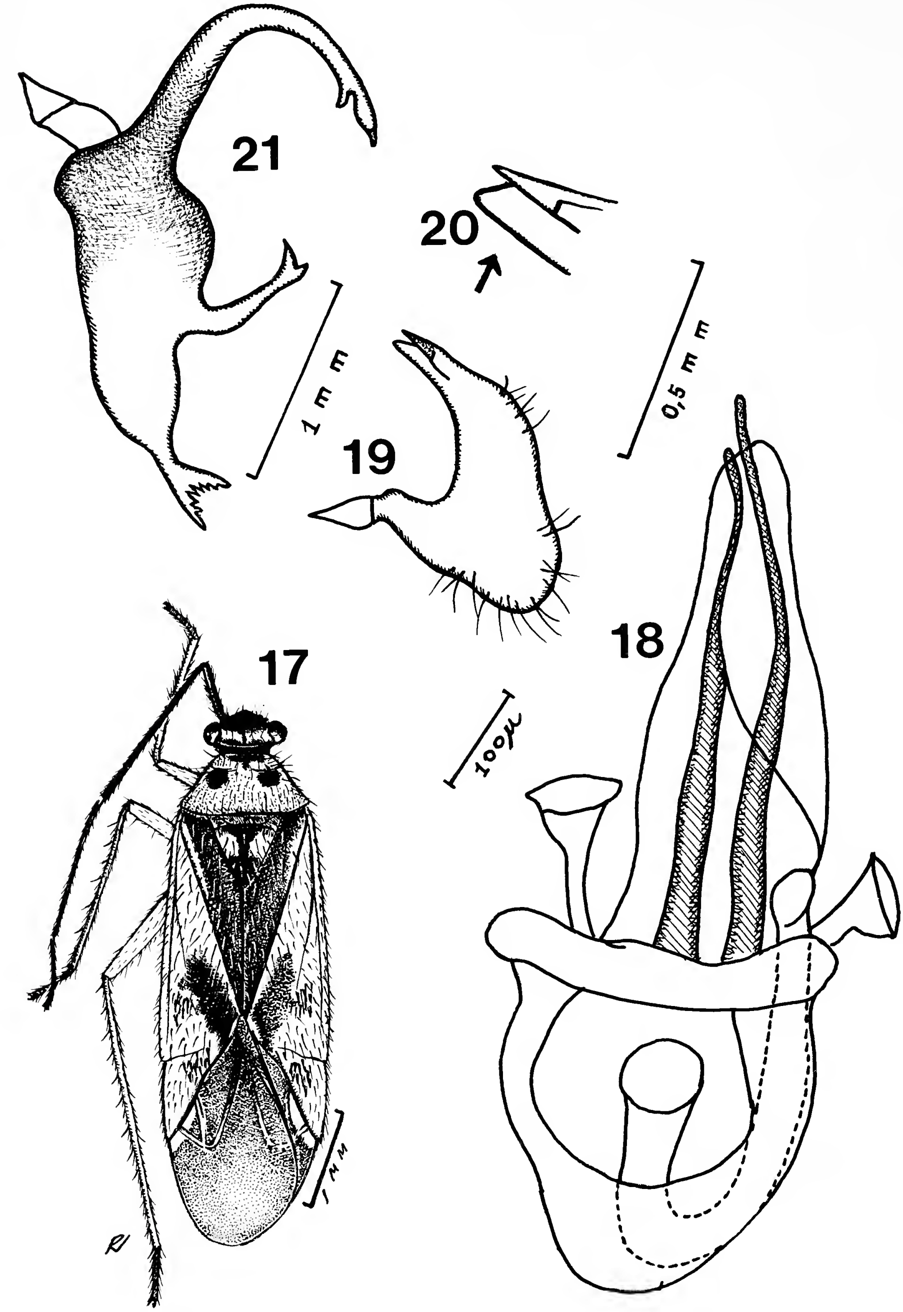
Fig. 14–16. 14. *Neofurius albiceps*, female, lectotype. 15, 16. *Paraguayna paraguayensis*. 15. Habitus. 16. Head and pronotum from above.

Male: Unknown.

Specimens examined. ♀ (herein designated as lectotype), Guadeloupe, Delauney, *Eroticoris albiceps* Lethiery, type, *Hallodapus albiceps* Lethierry, syntype, col, R. I. Sci. N. B.; ♀, (hereby designated as paralectotype), same data as for lectotype.

Paraguayna, new genus

Diagnosis. Has the general facies of *Eccritotarsus* Stål, 1860, but differs by having the scutellum totally covered by the hind margin of pronotum. It is closely related to the *Eccritotarsus* group of species in which some have the scutellum partially



Figs. 17–21. *Ilnacora arnaudi.* 17. Male, holotype. 18. Penis. 19. Left paramere. 20. Apex of left paramere. 21. Right paramere.

covered, such as *Eccritotarsus pilosus* Carvalho and Gomes, 1971. The genus *Pseudobryocoris* Distant, 1884 also has the scutellum almost covered by the pronotum; however, the shape of the hind margin is different.

Description. Body elongate, finely punctate, covered by fine, erect or semierect dense hairs.

Head wider than long, hind margin of vertex and frons rounded, antenna with segment I thicker than others, hairs about as long or longer than thickness of segment, segment II densely pilose, II and IV mutilated.

Pronotum characteristic, narrowed toward anterior end, wider at humeral angles (Figs. 15, 16), hind margin covex at sides and straight at middle, covering the scutellm and mesoscutum.

Hemelytra with thickened embolium and dense hairs on external margin, cuneus about twice as long as wide at base, membrane uniareolate.

Rostrum reaching the middle coxae, femora with long trichobothria, tibiae densely pilose.

Type species. Neofurius paraguayensis Carvalho and Drake, 1943.

Discussion. Based on the present generic criteria used to separate the genera of Bryocorinae, the author considers the species to represent a new genus in the tribe Eccritotarsini.

Etymology. The generic name taken after the country where the type was collected.

SUBFAMILY ORTHOTYLINAE

Tribe Orthotylini

Ilnacora arnaudi, new species

Figs. 17–21

Diagnosis. Differs from *Ilnacora chiuahuaensis* Knight and Schaffner, 1976, by morphology of the male genitalia, and the color of vertex and corium.

Description. Male: Length 5.4, width 1.6. *Head:* Length 0.3, width 0.9, vertex 0.46. *Antenna:* Segment I, length 0.5; II, 2.0; III 1.3; IV, 0.9. *Pronotum:* Length 0.7, width at base 1.3. *Cuneus:* Length 0.90, width at base 0.50 (holotype).

General coloration pale yellow to pale green with dark brown and black areas; head black, two large spots on vertex (one on each side) whitish, eyes (except posterior surface) and antenna black, extreme apex of antennal segment I, buccula, hind portion of lorum and antennal peduncle paler.

Pronotum pale yellow, collar and two spots behind calli black, mesoscutum and scutellum pale with longitudinal, wide, dark brown fascia that reaches apex of the latter.

Hemelytra pale greenish, endocorium with two spots at sides of corial commissure (one each side) black, membrane fuscous, veins pale.

Underside of body dark brown to black, rostrum (except apex), coxae, and legs pale, tibiae toward apex and tarsi fuscous.

Body covered by long, fine, erect setae and semierect or erect hairs, black spots of pronotum and corium with black scales, vertex carinate, segment I of antenna noticeably thicker than II.

Genitalia: Aedeagus (Fig. 18) with a large basal plate and vesica with two spicular prolongations tapering toward the apex. Left paramere (Fig. 19) strongly curved and sclerotized, stout, with a subapical acute lobe (Fig. 20) and several dorsal setae. Right paramere (Fig. 21) with three elongate branches (each one with two slender sclerotized spines or points), middle portion widened.

Female: Similar to male in coloration and general aspect.

Holotype. ♂, MEXICO, Chihuahua, 37 mi S of Hidalgo de Parral, VIII.21.60, P. H. Arnaud, Jr., E. S. Ross, and D. C. Rentz; deposited in the California Academy of Sciences, San Francisco.

Paratypes. 2♂♂, 5♀♀, same data and depository as holotype.

Etymology. The specific name is dedicated to P. H. Arnaud, Jr., collector of this species and curator of insects, California Academy of Sciences, San Francisco.

ACKNOWLEDGMENTS

I wish to thank Dr. P. H. Arnaud, Jr., for sending some of the interesting species of neotropical Miridae included in this paper. The illustrations were made by Paulo Roberto Nascimento and Maria Lilia Gomide da Silva.

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J. New York Entomol. Soc. 94(2):217–225, 1986

MERINOCAPSUS FROESCHNERI, A NEW SPECIES OF PHYLINE MIRIDAE FROM WESTERN NORTH AMERICA, WITH NOTES ON THE GENUS (HETEROPTERA)

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Abstract.—*Merinocapsus froeschneri* is described as new. *Ankylotylus pallipes* Knight is transferred to *Merinocapsus*. The male genitalia are illustrated and compared and the distributions summarized for the three species currently placed in *Merinocapsus*.

Knight (1968) described *Merinocapsus ephedrae* as one of a number of species of Miridae in western North America recorded as occurring on species of *Ephedra*. Intensive collecting by me and colleagues over the last seven years has revealed that there is an additional undescribed species of *Merinocapsus* on *Ephedra*. In the present paper I describe this species as new, naming it in honor of Richard C. Froeschner, in recognition of his longstanding interest in, and contributions to, the Heteroptera fauna of North America. I also tranfer *Ankylotylus pallipes* Knight to *Merinocapsus*.

Merinocapsus Knight

Merinocapsus Knight, 1968:34.
Ankylotylus Knight, 1968:55. **New Synonymy.**

Diagnosis. Recognized by the characteristic phyline-type male genitalia, the pretarsus with setiform parempodia and small pulvilli, the at least partially dark pronotum and scutellum contrasting with the lighter hemelytra which range from completely white to entirely deep red, the short head with weakly bulging eyes, the setiform parempodia, the elongate claws with small pulvilli (Fig. 4), the weak to moderately strong sexual dimorphism with the hemelytra in the males extending well beyond the apex of the abdomen and those of the female shorter and often just covering the abdomen, the metathoracic scent-gland evaporatory area elongate and narrow (Figs. 5–7), and the form of the male genitalia with the vesica slender and sigmoid, the apex bifid terminating with two small apical spines, and the secondary gonopore subapical (Figs. 9, 11, 14, 17).

Similar in general appearance and form of sexual dimorphism to many species of *Europiella* Reuter, but distinguished by the small pulvilli which do not cover most of the ventral claw surface as in *Europiella*, the more slender metathoracic scent gland evaporatory area, and the bifid apex of the vesica.

Discussion. Knight (1968) did not provide differential diagnoses for *Merinocapsus* and *Ankylotylus*. The two genera, which came out in the same couplet in his key, were distinguished by the structure of the tylus in *Ankylotylus pallipes* and the color of the tibial spines. My examination of additional specimens of *pallipes* indicates that Knight's interpretation was in error and that in fact there are no substantial differences in tylus structure between *pallipes, M. ephedra* and *M. froeschneri.* Because of the similarities in the structure of the tylus, pretarsus, metathoracic scent-gland evaporatory area, and the vesica of the male I am treating the two genera as synonymous, *Merinocapsus* having page priority.

The three species here placed in *Merinocapsus* all breed exclusively on *Ephedra. Merinocapsus ephedrae* and *froeschneri* have been collected together at the same site on the same host species, as have *froeschneri* and *pallipes.* I am uncertain whether they occurred on the same plant. Known *Ephedra* host species include *aspera* Englem. ex Wats., *cutleri* Peebles, *nevadensis* S. Wats., *torreyana* S. Wats., and *viridis* Coville.

Nearly all known specimens of *Merinocapsus* have been collected on *Ephedra.* Of the approximately 320 specimens examined, only one was recorded from lights, and a few lacked host information. A single specimen recorded from *Astragalus* is obviously not an accurate host record.

Additional species from western North America known to feed exclusively on *Ephedra,* and often occurring with *Merinocapsus* species, include the mirines *Phytocoris becki* Knight, *Phytocoris ephedrae* Knight, and the orthotylines *Ephedrodoma multilineata* Polhemus and Polhemus. Knight (1968) also recorded *Phytocoris pulchricollis* Van Duzee, and *Lopidea scutata* Knight on *Ephedra.* It is not obvious from my field observations that these last two species are obligate *Ephedra* feeders. The Palearctic phyline genus *Nasocoris* Reuter contains 11 species, all of which feed on *Ephedra.*

Merinocapsus ephedrae Knight
Figs. 1, 5, 8–10, 11–13, 20

Merinocapsus ephedrae Knight, 1968:34.

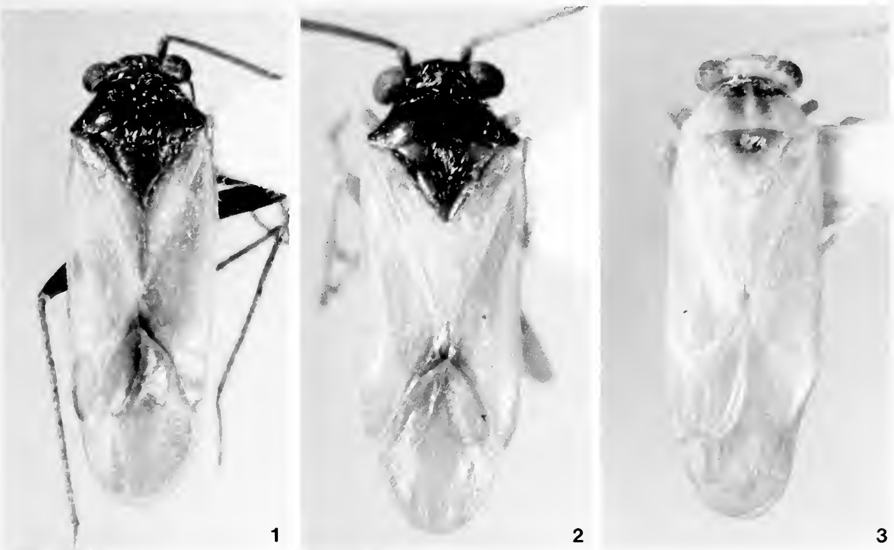
Diagnosis. Distinguished from *froeschneri* by the dull head, pronotum, and scutellum, the more elongate narrow body form, unicolorous dark femora, the generally infuscate tibiae, and the structure of the apex of the vesica (Figs. 9–11). Distinguished from *pallipes* by the completely dark head, pronotum, scutellum, venter, and legs, the hemelytral coloration with at least the cuneus reddish, the longer labium reaching to the apex of the mesocoxae, and the structure of the vesica.

Measurements: Total length: ♂, 3.45–4.31; ♀, 2.80–3.24. Length apex tylus-cuneal fracture: ♂, 2.27–2.83; ♀, 2.02–2.37. Width head: ♂, 0.79–0.86; ♀, 0.82–0.93. Width vertex: ♂, 0.37–0.42; ♀, 0.41–0.48. Width pronotum: ♂, 1.00–1.12; ♀, 0.95–1.10. Length pronotum at midline: ♂, 0.35–0.46; ♀, 0. 38–0.43. Length second antennal segment: ♂, 0.94–1.18; ♀, 0.76–0.92.

Male genitalia: Figures. 11–13.

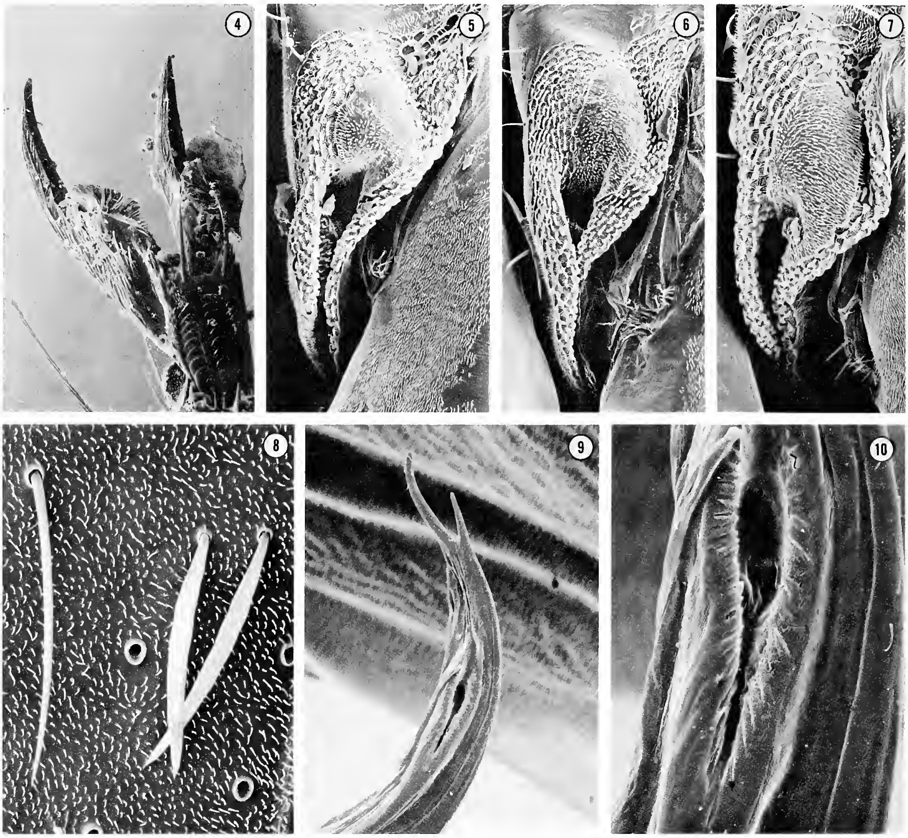
Distribution. Figure. 20. Northern Baja California north to Mono Lake, California, and east to eastern Utah.

Specimens examined. MEXICO. **Baja California Norte:** 12 mi E of El Rosario, March 25, 1979, John D. Pinto, on *Ephedra* (AMNH, UCR), 7♂♂, 5♀♀; 6 mi E of Ojos Negros, June 9, 1980, Brown, Faulkner (SDNHM), ♀. USA. **California:** *Inyo Co.:* Tuttle Creek, 2 mi SW of Lone Pine, May 9, 1969, P. A. Opler (UCB), ♂. 2 mi E of Westgard Pass Summit, White Mts., 2,125 m, July 2, 1980, R. T. Schuh, ex *Ephedra nevadensis* (AMNH), 6♀♀; Inyo Mts., May 25, 1937, D. Little (LACM), ♀.



Figs. 1–3. 1. *Merinocapsus ephedrae* ♂. 2. *Merinocapsus froeschneri* ♂. 3. *Merinocapsus pallipes* ♂.

Mono Co.: Wyman Canyon, White Mts., 2 airline mi S of Inyo, 8,500 ft, June 27, 1961, J. Powell, on *Ephedra* (UCB), 4♂♂, 2♀♀; Rt 395 at N edge of Mono Lake, 2,188 m, July 11, 1980, R. T. Schuh, G. M. Stonedahl, ex *Ephedra* sp. (AMNH), 3♂♂, 7♀♀. *Riverside Co.:* ca. 0.8 mi N of jct Deep Cr. and Horsethief Cr., T7S R6E Sec6, 2,960 ft, J. D. Pinto, Deep Canyon Project (UCR), ♂. *San Bernardino Co.:* 10 mi W of Lucerne Valley, 905 m, May 13, 1978, J. D. Pinto, R. T. Schuh, ex *Ephedra* sp. (AMNH, UCR), 6♂♂, 28♀♀; Providence Mts. State Rec. Area, 4,300 ft, May 18, 1982, M. D. Schwartz, ex *Ephedra aspera* (AMNH), 2♂♂, 6♀♀; 23 mi S of Amboy, April 7, 1966, C. W. O'Brien (UCB), 5♀♀; Victorville, April 21, 1935, C. E. Norland (LACM, UCD), 2♀♀. *San Diego Co.:* Anza-Borrego Desert State Pk., Grapevine Canyon, milepost 74 on Co. Rt 52, April 22, 1980, Russell and Schwartz (AMNH), ♂. **Nevada:** *Lincoln Co.:* 5 mi NE of jct of rts 38 and 93, 2,500 ft, May 19, 1982, M. D. Schwartz, ex *Ephedra nevadensis* (AMNH), 26♂♂, 18♀♀. *Nye Co.:* 1 mi NE of Belmont on Rt 82, 2,281 m, July 13, 1980, R. T. Schuh, G. M. Stonedahl, ex *Ephedra* sp. (AMNH), 7♂♂, 16♀♀; 15.5 mi E of Rt 376 on Northumberland Mine Rd, T31N R45E Secs3, 4, 10, 7,000 ft, June 29, 1983, Schuh, Schwartz, ex *Ephedra* sp. (AMNH), 17♂♂, 27♀♀; Mercury, 17M, June 12, 1965, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM), 2♂♂, 6♀♀ [paratypes]; Mercury, TM, June 14, 1965, Beck, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM), ♂, 9♀♀ [holotype, allotype, paratypes]; Mercury, 19M, June 23, 1965, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM), 3♀♀. **Utah:** *Garfield Co.:* Capitol Reef National Park, Grand Wash-Cobab Canyon Trl., 5,350–6,640 ft, June 21, 1983, Schuh, Schwartz, ex *Ephedra viridis* (AMNH), 2♂♂, 4♀♀; 14.3 mi S of Rt 95 on Rt 276 (3.4 mi N of Star Springs turnoff), 5,000 ft, June 19, 1983, R. T. Schuh, M. D. Schwartz, at light (AMNH), ♂. *Washington Co.:* Rt 15 about 10



Figs. 4–10. 4. Pretarsus of *M. pallipes*. 5–7. Metathoracic scent gland evaporatory area. 5. *M. ephedrae*. 6. *M. froeschneri*. 7. *M. pallipes*. 8. Setal types in *M. ephedrae*. 9. Apex of vesica in *M. ephedrae* showing secondary gonopore. 10. Detail of secondary gonopore.

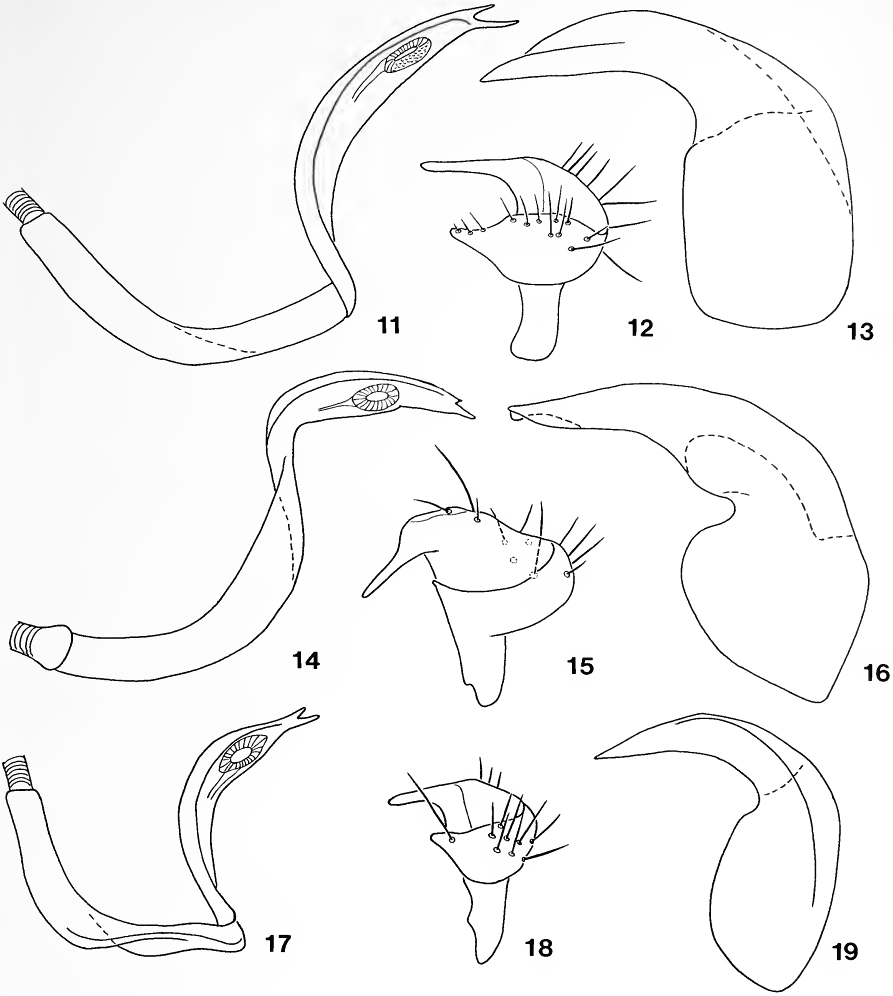
mi W of I-15 (toward Zion Nat. Pk.), 1,095 m, May 18, 1978, R. T. Schuh, ex *Ephedra* sp. (AMNH), 3♀♀.

Merinocapsus froeschneri, new species

Figs. 2, 6, 14–16, 20

Diagnosis. Distinguished from *ephedrae* by the polished and shining head, pronotum, and scutellum, the shorter broader body form, the apically pale femora and completely pale tibiae, and the structure of the apex of the vesica. Distinguished from *pallipes* by the completely dark head, pronotum, scutellum, the femora dark on the proximal two-thirds, the longer labium, reaching to about the apex of the mesocoxae, and the structure of the vesica.

Description. Macropterous. Elongate, nearly parallel-sided, total length 3.11–3.23, length apex tylus–cuneal fracture 2.17–2.22, head, pronotum, scutellum, entire pleura



Figs. 11–19. Male genitalia of *Merinocapsus*. 11–13. *M. ephedrae*. 11. Vesica. 12. Left paramere. 13. Phallotheca. 14–16. *M. froeschneri*. 14. Vesica. 15. Left Paramere. 16. Phallotheca. 17–19. *M. pallipes*. 17. Vesica. 18. Left paramere. 19. Phallotheca.

and venter, antennae, coxae, and about proximal two thirds of all femora dark brown to blackish.

Body surface polished, weakly to moderately shining, hemelytra smooth, dull to weakly shining; dorsum covered with pale, reclining, simple setae, and silvery, sericeous, flattened, recumbent setae; anterolateral angles of pronotum with an erect spine; antennae with short, neat vestiture; tibiae with scattered, suberect black spines without black bases; tibiae without rows of tiny black spicules.

Head short, broad, width 0.87–0.90, width vertex 0.40–0.41; posterior margin of vertex weakly elevated in form of a rounded carina; eyes bulging laterally, occupying about four fifths of height of head; antennae inserted just above ventral margin of eye; antennal segment two cylindrical, length 0.84–0.89; apex of labium not quite attaining apex of mesocoxae; pronotum with distinct calli, occupying anterior one third of pronotum; anterior and posterior pronotal lobes demarcated by a shallow transverse impression, lateral pronotal margin sinuous, posterior margin excavated across broadly exposed mesoscutum; width pronotum 1.00–1.08, length at midline 0.44–0.49; costal margin of hemelytra nearly straight, hemelytral margins nearly parallel-sided; cuneal incisure shallow; parempodia setiform, claws elongate, broadened basally, sharply bent near apex, pulvilli small.

Male genitalia: Figures. 14–16.

Female: Submacropterous. Similar in coloration, texture, and vestiture to male; antennal segment two tapering towards base; hemelytra distinctly shorter than in male, just covering entire abdomen.

Total length 2.94–3.08; length apex tylus cuneal fracture 2.05–2.21; width head 0.88–0.93; width vertex 0.43–0.47; width pronotum 1.01–1.10; length pronotum at midline 0.41–0.47; length second antennal segment 0.79–0.93.

Female genitalia: Not examined.

Etymology. Named in honor of Richard C. Froeschner.

Distribution. Figure. 20. Southern Mojave Desert in California north to White Mountains, and east to eastern Utah.

Holotype. ♂, USA. **California:** *Inyo Co.:* 2 mi E of Westgard Pass Summit, White Mts., 2,125 m, July 2, 1980, R. T. Schuh; deposited in the American Museum of Natural History, New York.

Paratypes. Same data as holotype, 7♂♂, 12♀♀ (AMNH). USA: **California:** *Mono Co.:* Benton Hot Springs, June 8, 1966, W. Gagne (UCB), 3♀♀. *Kern Co.:* 20 mi NW of Mojave, on Hiway 58, June 13, 1983, G. M. Stonedahl, ex *Ephedra nevadensis* (AMNH), ♂, 4♀♀; *San Bernardino Co.:* Yucca Valley, 6.3 mi N on Old Woman Springs Road, May 13, 1978, J. D. Pinto, on *Ephedra* (UCR), ♂, ♀; Providence Mts. State Rec. Area, 4300 ft, May 18, 1982, M. D. Schwartz, ex *Ephedra viridis* (AMNH), 3♂♂; 10 mi N of Yucca Valley, May 28, 1975, J. D. Pinto, on *Ephedra* (UCR), ♀. *Los Angeles Co.:* Little Rock, Mojave Desert, May 20, 1937, E. P. Van Duzee (CAS), ♂; Mint Canyon, May 17, 1937, E. P. Van Duzee, on *Astragalus* (CAS), ♀. Tehachapi Pass, June 6, 1929, R. L. Usinger (CAS), 5♀♀. **Nevada:** *Lincoln Co.:* 5 mi NE of jct. Rts 38 and 93, 2,500 ft, May 19, 1982, M. D. Schwartz, ex *Ephedra nevadensis* (AMNH), 3♂♂. *Nye Co.:* Nevada Atomic Test Site, Mercury Hwy at Angle Rd (A3), 3,800 ft, June 8, 1983, Schuh, Schwartz, Stonedahl, ex *Ephedra nevadensis* (AMNH), 11♂♂, 28♀♀; Nevada Atomic Test Site, 1 mi S of Cane Springs Rd, at GS 250 on Rd 28-03 (A5), 4,100 ft, June 8, 1983, Schuh, Schwartz, Stonedahl, ex *Ephedra nevadensis* (AMNH), ♂, ♀; Mercury, CU, June 13, 1965, Beck, Knight, Merino (USNM), 4♀♀ [*ephedrae* paratypes]; Mercury, 6M, June 15, 1965, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM), 2♀♀ [*ephedrae* paratype]; Mercury, TM, June 14, 1965, Beck, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM), 3♀♀ [*ephedrae* paratypes]; Mercury, CM, June 13, 1965, Beck, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM), ♀; Mercury, 18M, July 7, 1965, E. Beck, J. Merino, on *Ephedra nevadensis* (USNM), ♀ [*ephedrae* paratype]; Mercury, 40M, June 20, 1965, H. Knight,

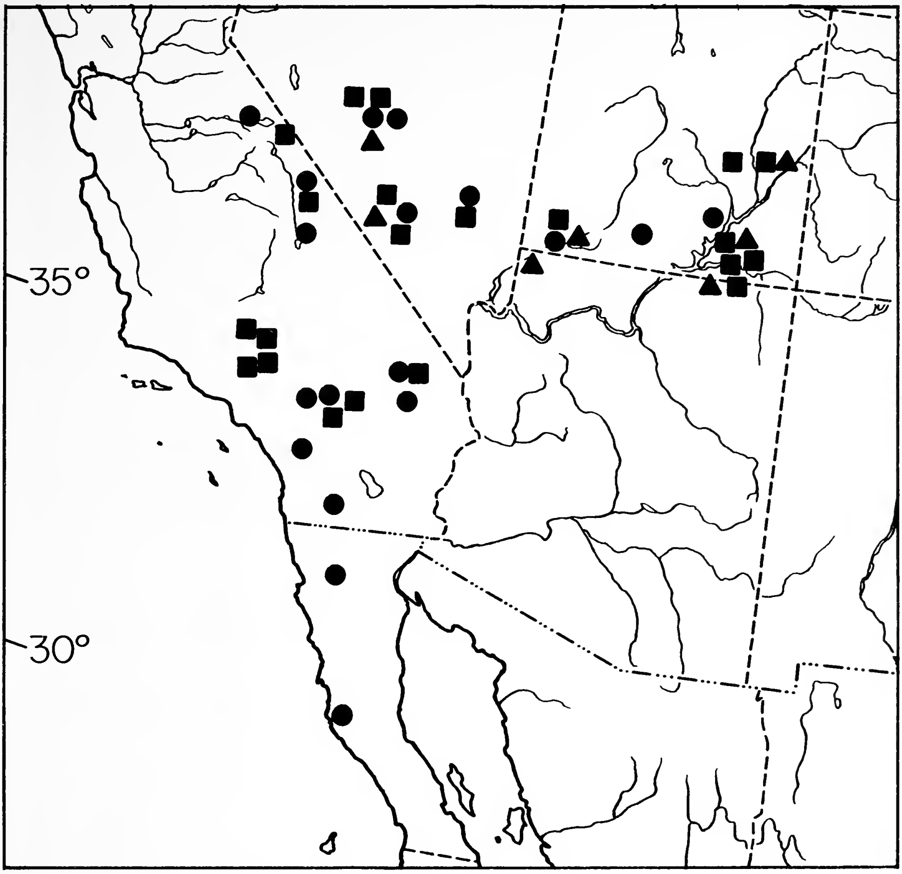


Fig. 20. Distribution of *Merinocapsus* species: ●, *ephedrae;* ■, *froeschneri;* ▲, *pallipes.*

J. Merino, on *Ephedra nevadensis* (USNM), 3♀♀ [*ephedrae* paratypes]; 5 mi E of Gabbs on Rt 844, 5,800 ft, July 1, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra* sp. (AMNH), ♂, 6♀♀; Northumbland Canyon Rd, Toquima Mts., T14N R44E Sec31, 6,400 ft, June 28, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra* sp. (AMNH), 4♂♂, 6♀♀. **Utah:** *Emery Co.:* 2.5 mi W of Rt 24 on Goblin Valley Rd, 5,500 ft, June 19, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra cutleri* (AMNH), ♂. *Grand Co.:* 11 mi SE of jct. Rts 313 and 163 on Rd 313 (road to Dead Horse Point), 5,200 ft, June 11, 1982, M. D. Schwartz, ex *Ephedra viridis* (AMNH), 13♂♂, 35 ♀♀. *San Juan Co.:* Rt 63 at Arizona border, Monument Valley, 5,200 ft, June 16, 1983, Schuh, Schwartz, ex *Ephedra cutleri* Peebles (AMNH), 13♂♂, 53 ♀♀; 12 mi S of Rt 263, Glen Canyon Nat. Rec. Area, T40S R14E, 4,300 ft, June 17, 1983, R. T. Schuh, M. D. Schwartz, ex Mercury Vapory light (AMNH), ♂; The Goosenecks Overlook, 5,000 ft, June 17, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra torreyana* S. Wats. (Ephedraceae) (AMNH), 4♂♂, ♀; Grand Flat, near Collins Canyon, 5,600 ft, May 28, 1978, D. A.

and J. T. Polhemus (AMNH, JTP), 4♂♂, 5 ♀♀; Head of Lake Canyon near Nokai Dome Road, 4,200 ft, May 29, 1978, D. A. and J. T. Polhemus (AMNH), ♂, ♀; 2.7 mi W of Rt 95 on Rt 263, T37S R17E, 6000 ft, June 18, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra torreyana* (AMNH), 2♂♂; 7.7 mi N of Mexican Hat on Rt 261, T41S R18E, 5,000 ft, June 17, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra* sp. (AMNH), ♀. *Washington Co.:* 2 mi NW of Toquerville on Utah St. Rd 17, 3,800 ft, May 25, 1981, M. D. Schwartz ex *Ephedra viridis* (AMNH), ♀.

Merinocapsus pallipes (Knight), **New Combination**

Figs. 3, 4, 7, 17–20

Ankylotylus pallipes Knight, 1968:56.

Diagnosis. Distinguished from *ephedrae* and *froeschneri* by the pale head, hemelytra, venter and legs, the pronotum and scutellum partially suffused with red-orange, the labium reaching only about midway between the pro- and mesocoxae, and the structure of the vesica (Fig. 17).

Measurements: Total length: ♂, 3.55–3.75; ♀, 2.95–3.26, length apex tylus–cuneal fracture: ♂, 2.37–2.40; ♀, 2.12–2.22. Width head: ♂, 0.84–0.87; ♀, 0.82–0.85. Width vertex: ♂, 0.34–0.35; ♀, 0.40–0.41. Width pronotum: ♂, 0.95–1.00; ♀, 1.01–1.03. Length pronotum at midline: ♂, 0.39–0.44; ♀, 0.39–0.40. Length second antennal segment: ♂, 0.92–0.94; ♀, 0.84–1.04.

Male genitalia: Figures. 17–19.

Distribution. Figure 20. Southern Nevada, northeastern Arizona, east to eastern Utah.

Specimens examined. USA: **Arizona:** *Coconino Co.:* 27 mi E of Jacob Lake on Rt 89 Alt., June 24, 1980, R. T. Schuh, ex *Ephedra torreyana* (AMNH), ♂, 2♀♀. *Mojave Co.:* Virgin River Canyon, 0.35 mi SW of milepost 24 on Hiway 15, Purgatory Canyon, 2,600 ft, May 24, 1981, M. D. Schwartz, ex *Ephedra* sp. (AMNH), 2♂♂. **Nevada:** 35 mi N of Tonopah, Coyote Hole Spg./Sevier Resrvr., T8N R42E Secs11, 23, 6,000 ft, June 30, 1983, Schuh, Schwartz, ex *Ephedra* sp. (AMNH), 4♀♀; Northumbland Canyon Rd, Toquima Mts., T14N R44E Sec31, 6,400 ft, June 28, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra* sp. (AMNH), 5♂♂, 6♀♀; *Nye Co.:* Mercury, 401M, June 20, 1965, H. Knight, J. Merino, on *Ephedra nevadensis* (USNM) ♂ [holotype]; Mercury, TM, June 14, 1965, Beck, H. Knight, J. Merino (USNM), ♀ [paratype]. **Utah:** *Grand Co.:* 11 mi SE of jct. Rds 313 and 163 on Rd 313 (road to Dead Horse Point), 5,200 ft, June 11, 1982, M. D. Schwartz, ex *Ephedra viridis* (AMNH), ♂, 2♀♀. *San Juan Co.:* The Goosenecks Overlook, 5,000 ft, June 17, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra torreyana* S. Wats. (Ephedraceae) (AMNH), 7♂♂, 11♀♀; 1.2 mi W of Jct of Gooseneck Rd on Co. Rt 244, 5,000 ft, June 16, 1983, R. T. Schuh, M. D. Schwartz, ex *Ephedra torreyana* S. Wats. (Ephedraceae) and ex mercury vapor light (AMNH), 3♂♂, 4♀♀; 12 mi S of Rt 263, Glen Canyon Nat. Rec. Area, T40S R14E, 4,300 ft, June 17, 1983, R. T. Schuh, M. D. Schwatz, ex *Ephedra torreyana* S. Wats. (Ephedraceae) (AMNH), ♂, 5♀♀; Rt 63 at Arizona border, Monument Valley, 5,200 ft, June 16, 1983, Schuh, Schwartz, ex *Ephedra cutleri* Peebles (Ephedraceae) (AMNH), 4♂♂, 7♀♀. *Washington Co.:* 3.5 mi E of La Verkin, June 25, 1980, R. T. Schuh, ex *Ephedra* sp. (AMNH), 2♀♀.

ACKNOWLEDGMENTS

I thank the following individuals for making material available from collections in their charge (institutional abbreviations used in locality data as indicated): Paul Arnaud (California Academy of Sciences; CAS), Julian Donahue (Natural History Museum of Los Angeles County; LACM), John T. Polhemus (Englewood, Colorado; JTP), John Chemsak (University of California, Berkeley; UCB), Robert Schuster (University of California, Davis; UCD), John Pinto (University of California, Riverside; UCR), David Faulkner (San Diego Museum of Natural History; SDNM), and Thomas J. Henry (Systematic Entomology Laboratory, USDA, % National Museum of Natural History, Washington, D.C.; USNM). I also thank Jeff Knight, Nevada State Entomologist and the authorities of the Nevada Atomic Test Site for permission to collect on the Test Site and the authorities at Capitol Reef National Park for permission to collect in the Park. I especially thank Michael Schwartz for technical assistance and Michael Schwartz and Gary Stonedahl for field assistance and helpful discussions. The staff of the New York Botanical Garden, Bronx, New York, particularly Jackie Kallunki and Eileen Schofield, provided host identifications. Support for field work and technical assistance was received from NSF Grant DEB 81-13401.

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STYLOPOMIRIS, A NEW GENUS AND THREE SPECIES OF ECCRITOTARSINI (HETEROPTERA: MIRIDAE: BRYOCORINAE) FROM VIET NAM AND MALAYA

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Abstract.—The genus *Stylopomiris* and the included species *froeschneri, indochinensis,* and *malayensis* are described as new. The male genitalic structures of all species are illustrated, and a dorsal habitus provided for the female of *malayensis.* Scanning electron micrographs of the metaepisternal scent efferent system and the pretarsal structure document the placement of the genus in the tribe Eccritotarsini.

An ongoing study of the Eccritotarsini of the Old World has revealed three undescribed, congeneric species that cannot be placed in any known genus of the tribe. In the present paper, I describe the genus *Stylopomiris* and the included species *froeschneri, indochinensis,* and *malayensis* as new. The first species is named in honor of Richard C. Froeschner in recognition of his contributions to the study of Heteroptera and service as curator of Hemiptera at the National Museum of Natural History, Washington, D.C.

Stylopomiris, new genus

Diagnosis. Recognized by the broad head with moderately to strongly stalked eyes (Fig. 1); short, thin antennae; long labium; large, single cell of hemelytral membrane with strong loop-like apex (Fig. 1); and by the structure of the male genitalia, especially the broad right paramere (Figs. 13–15) and elongate, curved shaft of the left paramere (Figs. 10–12).

Description. Macropterous male. Length (apex of tylus to apices of hemelytra) 3.28–4.10 (all measurements are in millimeters); width across humeral angles of pronotum 0.90–1.14; creamy white or pale brownish yellow general coloration with brown to fuscous markings; surface texture granular, slightly shining, posterior lobe of pronotal disk and propleura punctate; dorsal vestiture of moderately long, suberect, fine simple setae (more densely distributed on head). HEAD. Broad, short, frons and tylus projecting slightly beyond anterior margin of eyes in dorsal view; frons moderately convex, junction with tylus narrowly depressed; vertex broad, transversely flattened, sometimes slightly excavated anteriorly, eyes moderately to strongly stalked, projecting laterally to well beyond anterolateral angles of pronotum, and posteriorly to near level of calli; eye stalks usually broadening distally and projecting above level of vertex; eyes small, slightly compressed dorsoventrally, elongate in dorsal view, occupying only one-third of head height in lateral view; antennae inserted at or below ventral margin of eyes; antennal fossae small, well removed from anterior margin of eyes; antennal segment one about as long as length of eye in dorsal view, length of segment two less than width of head across eyes, segment three and segment four slightly longer than segment two; all antennal segments cylindrical, linear, clothed with moderately long, suberect simple setae, segment one thicker than segments 2–4, segment two sometimes slightly expanded distally; juga and lora broad, slightly swollen; genal region broad, developed into eye stalk; bucculae short, triangular, buccal cavity subspherical; gula obsolete; labium reaching metacoxae or slightly beyond, segments one and two similar in length, slightly more than twice as long as segments three and four. PRONOTUM. More or less trapezoidal with well-defined anterior and posterior lobes; posterior lobe moderately swollen, projecting over base of scutellum; anterior margin with well-developed flattened collar about as broad as or broader than diameter of antennal segment one, posterior margin of collar with moderate to deep transverse depression either side of midline; calli well-developed, usually rising abruptly from collar, reaching lateral margins of pronotum, separated anteromedially by pair of deep circular depressions; lateral margins of disk sinuate, with distinct concavity at level of posterior margin of calli, lateral juncture of collar and calli strongly recessed; posterior margin of disk slightly arcuate medially, broadly rounded laterally; mesoscutum concealed; scutellum weakly elevated, slightly transversely rugulose; metathoracic scent efferent system with tongue-shaped peritremal disc along posterior margin of metaepisternum, disc with weak central canal extending from minute ventral osteole between meso- and metacoxae. HEMELYTRA. Elongate, weakly rounded laterally; embolium swollen; cuneus about twice as long as broad, cuneal fracture and incisure weak; membrane with large single cell, posterior margin of cell broadly loop-like. LEGS. Femora elongate, slightly flattened to nearly cylindrical; meso- and metafemora nearly linear, sometimes slightly expanded near distal trichobothria; profemora more robust, narrowly rectangular, tapering slightly distally; tibiae cylindrical, protibiae flared distally; femora and tibiae clothed with reclining, pale simple setae; tarsi dilated distally, segments similar in length; claws moderately curved, broad basally with large fleshy disc-like pulvillus attached to inner surface, posteroventral margin of pulvillus with comb-like row of long trichia; parempodia long, setiform. GENITALIA. Genital capsule: large, deep, with broad posterodorsally oriented aperture, lateral margins bordering aperture sometimes with spine-like or plate-like sclerite above paramere socket; ventral region between paramere sockets with well-developed sling-like sclerite supporting vesica. Left paramere: sensory lobe well-developed, tapering to broadly U-shaped angle; shaft very long, narrow, variously curved. Right paramere: short, broad, apex rounded or truncate with small dorsal spine or serration. Vesica: ductus seminis entirely membranous; single, weakly curved vesical process with reflexed margins, sometimes nearly tubular, basal region with finger-like process, inner distal margin sometimes with flattened process, apex rounded with multilobed membranous sack originating from small to moderate-sized medial pore.

Female: Macropterous. Similar to male in color, vestiture, and structure except hemelytra slightly more rounded laterally. Genitalia not examined. Only the female of *malayensis* is known (Fig. 1).

Etymology. From the Greek *stylos* (pillar), *ops* (eye), and *miris,* referring to the moderately to strongly stalk-eyed condition of members of the genus; masculine.

Type species. Stylopomiris malayensis, new species.

Distribution. South Viet Nam and Malaya (Fig. 2).

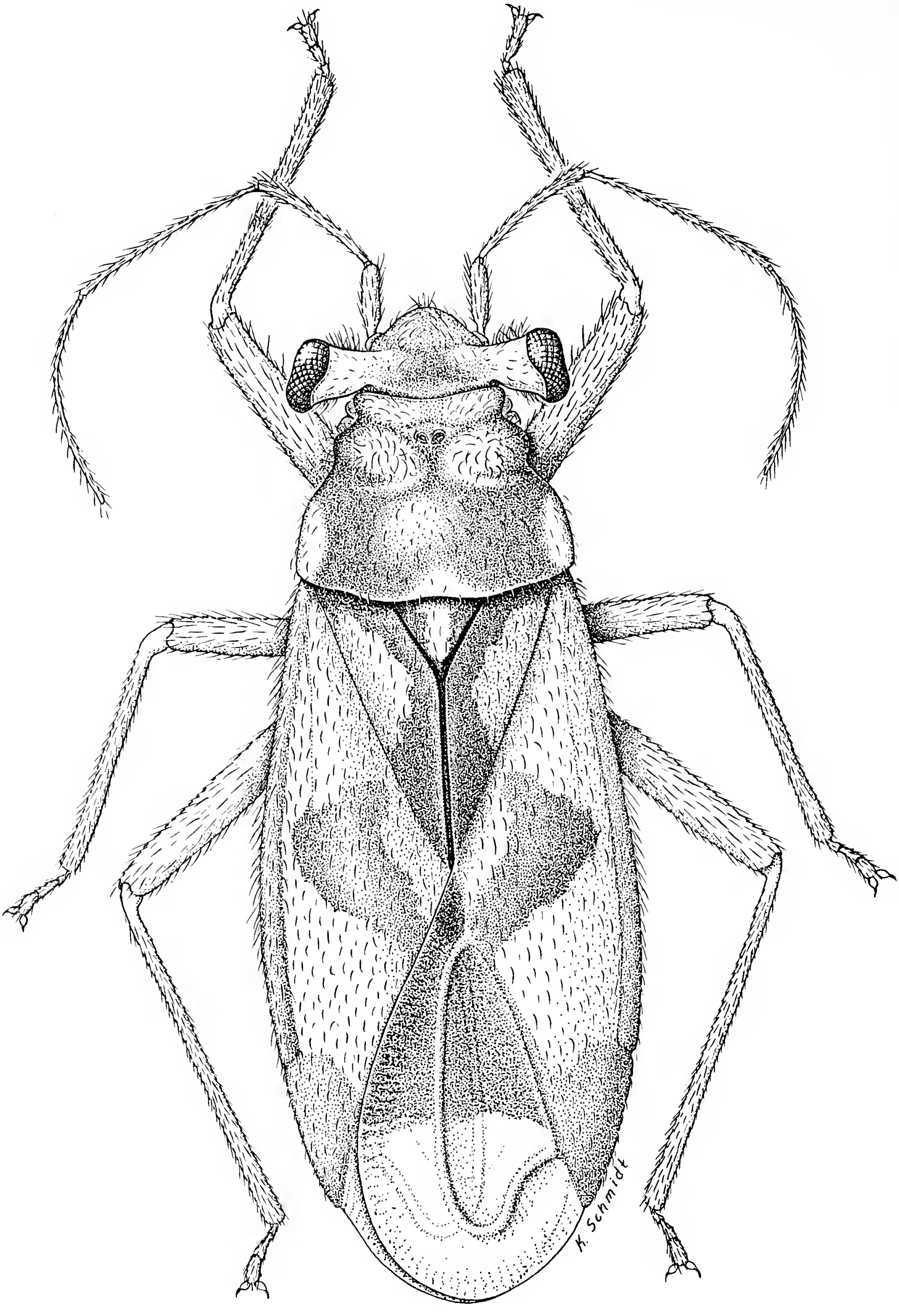


Fig. 1. *Stylopomiris malayensis*, dorsal habitus of female.

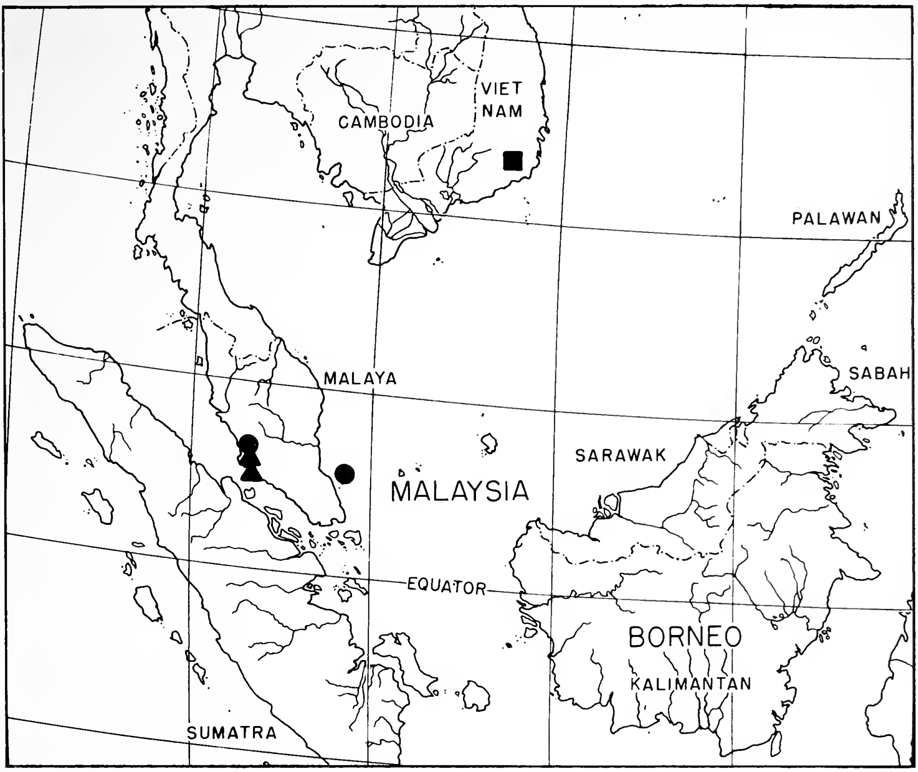
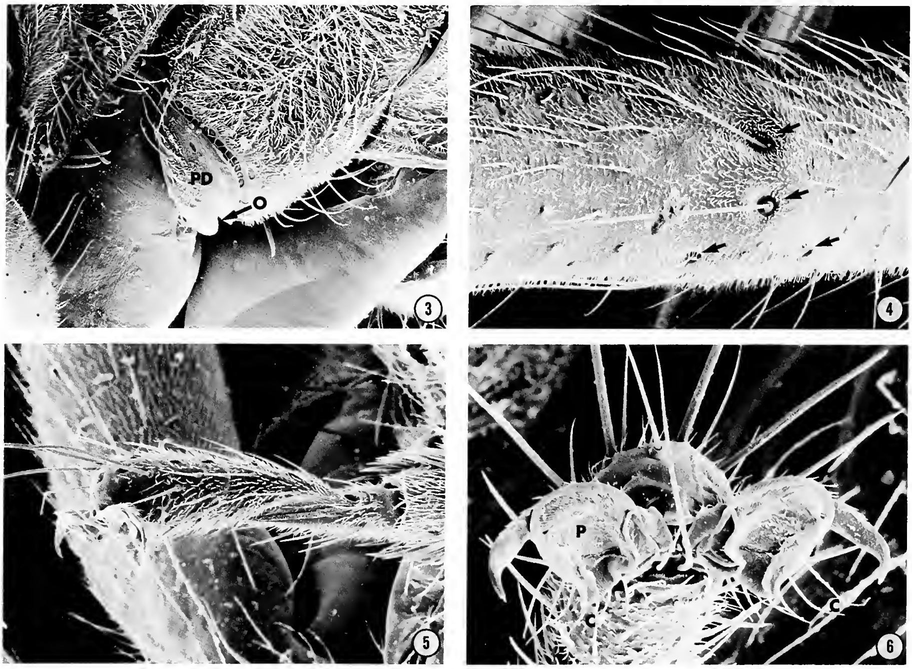


Fig. 2. Distribution of *Stylopomiris froeschneri* ▲, *S. indochinensis* ■, and *S. malayensis* ●.

Discussion. Stylopomiris is recognized as belonging to the tribe Eccritotarsini by the structure of the metaepisternal scent efferent system (Fig. 3), metafemur swollen at point of insertion of distal trichobothria (Fig. 4), morphology of the pretarsus (Fig. 6), and structure of the male genitalia, especially the vesica (Figs. 16–18)(see generic description for explanation). It is distinguished from other members of the tribe by the characters given in the generic diagnosis.

The relationship of *Stylopomiris* to other eccritotarsines is uncertain. In Carvalho's (1955) key to genera of Miridae of the World, it runs to couplet six containing *Hesperolabops* Kirkaldy and *Neoleucon* Distant because of the strongly stalked eyes. However, *Stylopomiris* is not closely related to these taxa, or to other New World members of the tribe.

Stylopomiris superficially resembles several Old World genera with stalked eyes (e.g., *Prodromus* Distant, *Thaumastomiris* Kirkaldy, *Stenopterocoris* China), but overall seems more closely related to a complex of genera that share the following attributes: 1) small body size, 2.5–4.6 mm; 2) moderately to strongly inflated posterior lobe of the pronotal disk that projects over the base of the scutellum; 3) paramere sockets with prominent, sometimes inflated, processes on inner margin; and 4) right paramere short and broad. The genera possessing these features are *Eofurius* Poppius, *Ernes-*



Figs. 3–6. *Stylopomiris malayensis.* 3. Metaepisternal scent efferent system (O, osteole; PD, peritremal disk). 4. Distal trichobothria of metafemur. 5. Metatarsus. 6. Pretarsus (P, pulvillus; C, pulvillar comb).

tinus Distant, *Microbryocoris* Poppius, *Myiocapsus* Poppius, and *Palaeofurius* Poppius.

The host plant associations of *Stylopomiris* species are not known.

Stylopomiris froeschneri, new species

Figs. 2, 7, 10, 13, 18

Diagnosis. Recognized by the prominent subtriangulate eye stalks, strongly projecting above level of vertex; length of second antennal segment equal to or slightly greater than width of vertex; width of pronotal collar equal to diameter of antennal segment one; and by the structure of the male genitalia, especially the right paramere with strong basodorsal spine (Fig. 13) and vesica without flattened process on inner distal margin (Fig. 18). Similar to *malayensis* in general coloration but with pronotal disk mostly pale and corium with pair of transverse fuscous marks, one about halfway between cuneal fracture and apices of clavi, and one slightly above level of apices of clavi.

Description. Male. Length 4.10; general coloration and dorsal vestiture as in generic description. HEAD. Width across eyes 1.04–1.08, width of vertex 0.65–0.66; brownish yellow, tylus and apex of frons darker yellowish brown; eyes produced on prominent subtriangulate stalks, strongly elevated above level of vertex; vertex broadly depressed anteriorly; antennae pale yellow or brownish yellow, inserted well below ventral margin of eye, length of segment one 0.26–0.28, segment two 0.66–0.72; labium reaching slightly beyond apices of metacoxae. PRONOTUM. Posterior width 1.08–1.14; pale brownish yellow; collar, narrow region between and behind calli, and posterior margin of disk, except medially, brown or dark brown; width of collar subequal to diameter of antennal segment one; calli prominent, rising abruptly from depressions behind collar; posterior lobe of disk with longitudinal depressed region bordering lateral margins; scutellum pale with dark patch medially. HEMELYTRA. Creamy white; inner margin and distal half of clavus, anal ridge, and cuneus dark brown; corium with pair of dark transverse marks, one slightly above level of apices of clavi, one equidistant between cuneal fracture and apices of clavi; exocorium yellowish brown with dark brown mark medially; membrane suffused with fuscous to slightly beyond level of cuneal fracture. LEGS. Femora yellowish brown, slightly darker distally; tibiae pale brownish yellow; tarsi and claws yellowish brown. GENITALIA. Figures 7, 10, 13, 18. Right paramere with strong dorsal spine basally (Fig. 13).

Female: Unknown.

Etymology. Named for Richard C. Froeschner.

Distribution. Figure 2. Malaya.

Holotype. ♂ MALAYSIA. **Malaya.** *Selangor Prov.:* Weld Hill F. R., Kuala Lumpur, October 8, 1932, H. M. Pendlebury collector; deposited in the British Museum (Natural History), London.

Paratypes. ♂ (poor condition, discolored and with hemelytra missing), MALAYSIA, **Malaya,** *Negri Sembilan Prov.,* Port Dickson, March 1, 1935, H. M. Pendlebury (BM).

Stylopomiris indochinensis, new species

Figs. 2, 8, 12, 14, 16

Diagnosis. Recognized by the less prominent eye stalks, not projecting above level of vertex, antennal segment two nearly as long as width of head across eyes; pronotal collar only slightly broader than diameter of antennal segment one; antennae and legs brownish; hemelytra extensively darkened; and by the structure of the male genitalia, especially the extremely long, thin shaft of the left paramere (Fig. 12), the kidney-shaped right paramere (Fig. 14), and the large sling-like support for the vesica between the paramere sockets (Fig. 8).

Description. Male. Length 3.90; brownish general coloration; dorsal vestiture as in generic description. HEAD. Width across eyes 0.86, width of vertex 0.51; yellowish brown; vertex, frons, and tylus fuscous; eyes less strongly stalked, not projecting above level of vertex; antennae brown, segment one more yellowish brown, inserted at level of ventral margin of eyes, length of segment one 0.26, segment two 0.71; labium reaching well beyond apices of metacoxae. PRONOTUM. Posterior width 1.06; grayish yellow, posterolateral angles broadly fuscous, calli brown; collar slightly broader than diameter of antennal segment one; calli moderately developed, rising gradually from collar; scutellum fuscous, with weak depression either side before narrowly pale apex. HEMELYTRA. Clavus fuscous except base, inner margin bordering scutellum, and apex narrowly pale; corium broadly darkened medially, basal and apical fourths and inner margin pale; cuneus and distal two-thirds of exocorium dark brown; membrane lightly suffused with fuscous proximally. LEGS. Femora yellowish brown basally, brown or dark brown distally; tibiae brown or yellowish brown, usually lighter apically; tarsi yellowish brown, claws golden brown. GENITALIA. Figures 8, 12, 14, 16. Left paramere with extremely long, thin shaft (Fig. 12).

Female: Unknown.

Etymology. Named for its occurrence in Indochina.

Distribution. Figure 2. South Viet Nam.

Holotype. ♂ VIET NAM. Fyan [Ngoc Son], 1,200 m, July 11–August 9, 1961, N. R. Spencer collector; deposited in the B. P. Bishop Museum, Honolulu.

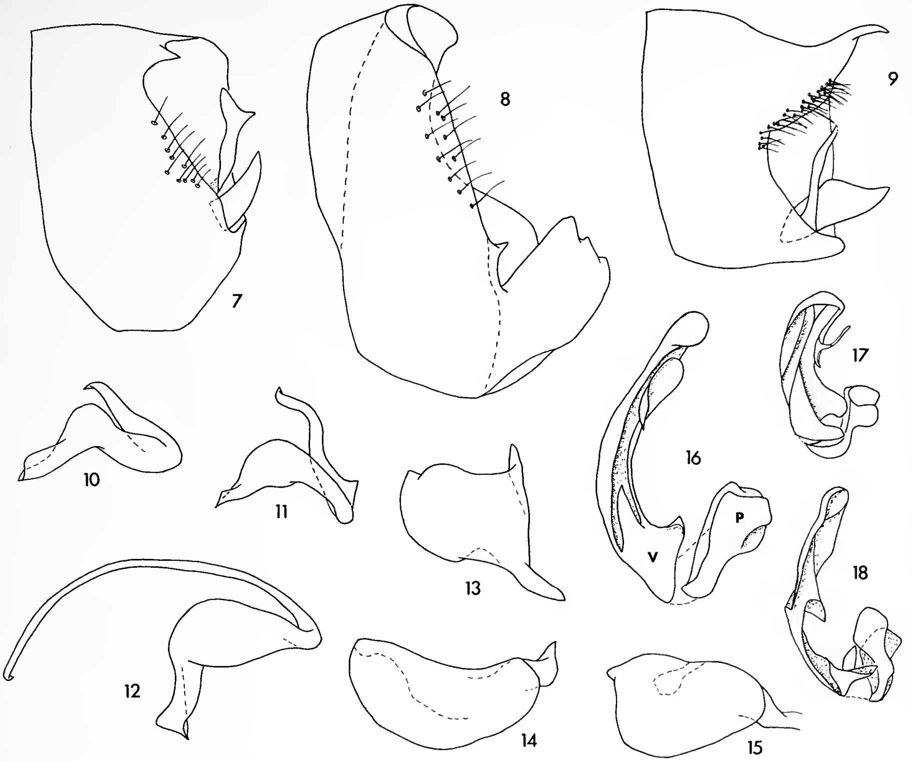
Stylopomiris malayensis, new species

Figs. 1–6, 9, 11, 15, 17

Diagnosis. Recognized by the prominent subtriangulate eye stalks, slightly produced above level of vertex; length of second antennal segment distinctly less than width of vertex; pronotal collar nearly twice as broad as diameter of antennal segment one; and by the structure of the male genitalia, especially the large acuminate process on the left lateral margin of the genital capsule (Fig. 9), and shape of the parameres (Figs. 11, 15). Distinguished from *froeschneri* by its smaller size, extensively darkened pronotal disk, short second antennal segment, less strongly elevated eye stalks, broad pronotal collar, and male genitalia.

Description. Male. Length 3.28–3.32; general coloration and dorsal vestiture as in generic description. HEAD. Width across eyes 0.99–1.00, width of vertex 0.66–0.68; brownish yellow, underparts slightly darker, apex of frons and tylus brown; eyes produced on prominent subtriangulate stalks, only slightly produced above level of vertex; antennae yellowish brown, inserted below ventral margin of eye; length of segment one 0.22–0.24, segment two 0.52; labium reaching slightly beyond apices of metacoxae. PRONOTUM. Posterior width 0.90–0.91; brown or dark brown; collar, posterolateral angles, and posterior margin mostly pale; collar nearly twice as broad as diameter of antennal segment one; calli prominent, rising abruptly from collar; scutellum dark brown, lighter yellowish brown medially. HEMELYTRA. Creamy white or pale yellow; clavus with basal fourth, inner margin, and apical third fuscous; corium with broad oblique fuscous patch reaching from anal ridge anteriorly to exocorium at level of apices of clavi; cuneus and most of exocorium brown or dark brown; membrane suffused with fuscous to near level of apex of cuneus. LEGS. Pale yellow or brownish yellow, only claws darker golden brown. GENITALIA. Figures 9, 11, 15, 17. Genital capsule with large, acuminate process on left lateral margin of aperture (Fig. 9).

Female: Figure 1. Similar to male in color, vestiture, and structure except hemelytra slightly more rounded laterally, calli sometimes pale on inner half, scutellum more broadly pale medially and apically, exocorium pale, and fuscous patch on corium not reaching costal margin (rarely extending laterally beyond radial vein). Length 3.50–3.65; width of head across eyes 1.00–1.03, width of vertex 0.68–0.69; length of antennal segment one 0.24–0.25, segment two 0.52; posterior width of pronotum 0.94–0.96.



Figs. 7–18. Male genitalic structures of *Stylopomiris* species. 7–9. Genital capsule, left lateral view. 7. *froeschneri.* 8. *indochinensis.* 9. *malayensis.* 10–12. Left paramere, lateral view. 10. *froeschneri.* 11. *malayensis.* 12. *indochinensis.* 13–15. Right paramere, lateral view. 13. *froeschneri.* 14. *indochinensis.* 15. *malayensis.* 16–18. Vesica (V) and phallobase (P) of aedeagus. 16. *indochinensis.* 17. *malayensis.* 18. *froeschneri.*

Etymology. Named for its occurrence in the state of Malaya.

Distribution. Figure 2. Malaya.

Holotype. ♂ MALAYSIA. **Malaya.** *Selangor Prov.:* Connaught Bridge, March 14, 1958, T. C. Maa collector; deposited in the B. P. Bishop Museum, Honolulu.

Paratypes. MALAYSIA. **Malaya.** *Selangor Prov.:* ♂, same data as holotype (BISH). Tioman Is.: 7♀♀, March 19, 1984, J. H. Martin (AMNH, BM).

ACKNOWLEDGMENTS

I thank Michael D. Webb (British Museum of Natural History; BM) and Wayne C. Gagné (Bernice P. Bishop Museum; BISH) for loaning specimens in their charge. I especially thank Kathy Schmidt for the fine dorsal illustration of *Stylopomiris malayensis,* and Michael D. Schwartz for technical assistance and helpful comments on the manuscript. Support for this research was provided by a Postdoctoral Fellowship Award from the Kalbfleisch Fund, American Museum of Natural History.

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J. New York Entomol. Soc. 94(2):235–244, 1986

MELANORHOPALA FROESCHNERI (HETEROPTERA: TINGIDAE): A NEW LACE BUG FROM EASTERN UNITED STATES, WITH NOTES ON HOST PLANT AND HABITS, DESCRIPTION OF FIFTH INSTAR, AND KEY TO SPECIES OF THE GENUS

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Abstract.—The new species *Melanorhopala froeschneri* (Heteroptera: Tingidae) is described from Delaware, Kentucky, Maryland, North Carolina, and Tennessee, and compared with the three previously described species of the genus. The fifth instar is described and illustrated; notes are given on the bug's host plant, *Campsis radicans* (L.) Seem. (Bignoniaceae), and on its habits; and a key is provided to separate the known species of *Melanorhopala.*

While collecting in Delaware in 1982, we discovered three specimens of a lace bug tentatively identified as *Melanorhopala infuscata* Parshley. Later collecting of numerous adults and nymphs and the discovery of the host of this interesting bug revealed that we had an undescribed species. Prior to this study, only three species of *Melanorhopala* Stål were recognized: *M. balli* Drake, known from the holotype taken in Colorado; *M. infuscata* from the District of Columbia, Maryland, North Carolina, and Virginia; and *M. clavata* (Stål) widely distributed from New England west to Wyoming and Colorado, and south to Florida (Drake and Ruhoff, 1965; Horn et al., 1979).

Herein, we describe the new species *Melanorhopala froeschneri,* provide electron micrographs of the adult and an illustration and description of the fifth instar, give notes on the host plant and habits, and provide a key to separate the four known species of the genus.

We are honored to dedicate the name of this cryptic new tingid to our friend and colleague Richard C. Froeschner. We also gratefully acknowledge the help and advice he has given freely over the years. Although always busy with his research, curating of the National Hemiptera Collection, building literature files, and helping others with their sometimes almost overwhelming requests, Dick has always stopped his own pursuits to cheerfully help us with our inquiries and problems or to offer welcomed philosophical thought that only he can generate.

Genus *Melanorhopala* Stål

Tingis (*Melanorhopala*) Stål, 1873:130.
Melanorhopala: Horvath, 1908:564.

Diagnosis. Generally elongate, hemelytra subparallel in macropterous males, elongate oval in females and brachypterous specimens; head quadrate, armed with five elongate, decurved spines (Figs. 3, 4), bucculae greatly expanded, rectangular in lateral view, contiguous anteriorly but not fused, extending length of head to near front of acetabula just under anterior margin of pronotum (Fig. 4); antennae cylindrical, slightly thickened, segment III longest, often clavate apically, segments I and II short, barrel-shaped, segment IV fusiform; pronotum tricarinate, lacking a raised hood, paranota narrow, reflexed, and flattened against pronotum; hemelytra uniformly areolate, apices quadrate and slightly rounded in macropterous forms, apically acuminate and diverging in brachypterous specimens, costal area with one or two rows of areoles.

Type species. Tingis clavata Stål, 1873; fixed by Van Duzee, 1916: 26.

Remarks. Melanorhopala is most closely related to the genera *Alveotingis* Osborn and Drake and *Hesperotingis* Parshley. It can be distinguished as follows: *Alveotingis* with antennal segment III uniformly thickened, hemelytra broadly rounded apically and laterally, discoidal area not bordered by a carina (or thickened veins); *Hesperotingis* with antennal segment III thickened on apical half, hemelytra broadly oval, rounded apically, discoidal area bordered by a carina; *Melanorhopala* with antennal segment III uniformly slender to slightly swollen on apical half, sometimes apically clavate, hemelytra subparallel to elongate oval, apically quadrate and slightly rounded in macropterous specimens, apically acuminate and diverging in brachypterous ones; discoidal area bordered by carina. Hurd (1946) provided a good diagnosis and key to these genera.

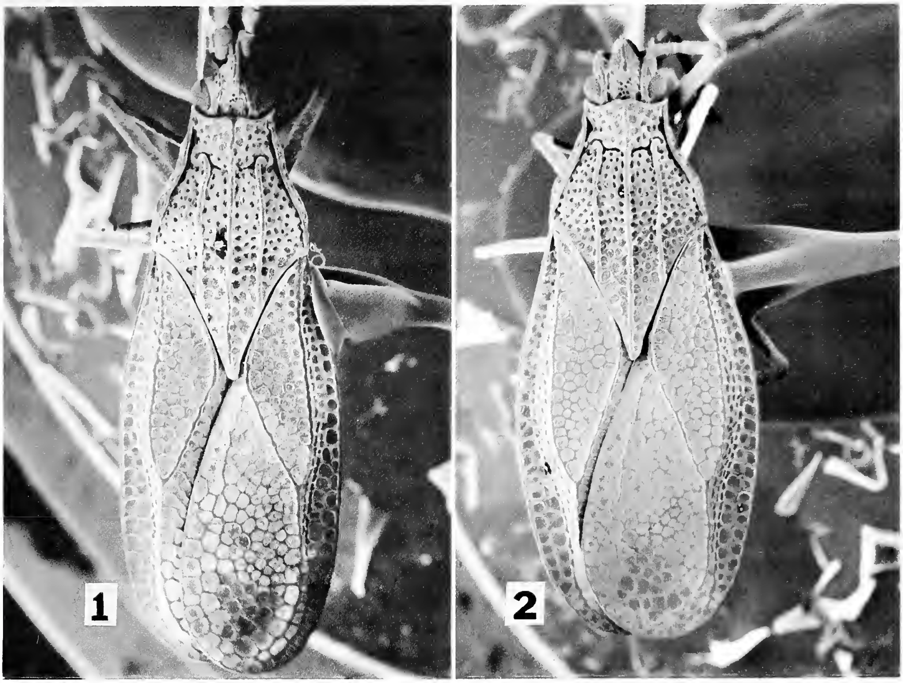
KEY TO SPECIES OF *Melanorhopala*

1. Rostrum extending to or beyond hind coxae 2
– Rostrum not extending beyond middle coxae 3
2. Antennal segment II distinctly shorter and more slender than segment I; antennal segment III uniformly slender (Figs. 8, 9); lateral height of eye distinctly less than distance from lower margin of eye to lower margin of buccula .... *infuscata* Parshley
– Antennal segment II subequal to length and thickness of segment I (Fig. 3); antennal segment III distinctly thicker on basal half (Figs. 6, 7); lateral height of eye distinctly greater than distance from lower margin of eye to lower margin of buccula (Fig. 4) . ... *froeschneri,* new species
3. Antennal segment I nearly 2 × length of segment II (Figs. 10, 11); segment III distinctly clavate apically in females (Fig. 11); length of segment III at least 4 × combined length of segments I and II; length 5.00 mm or more .... *clavata* (Stål)
– Antennal segment I only slightly longer than segment II (Fig. 5); antennal segment III not clavate apically (Fig. 5); length of segment III less than 3 × combined length of segments I and II; length 3.25 mm or less .... *balli* Drake

Melanorhopala froeschneri, new species

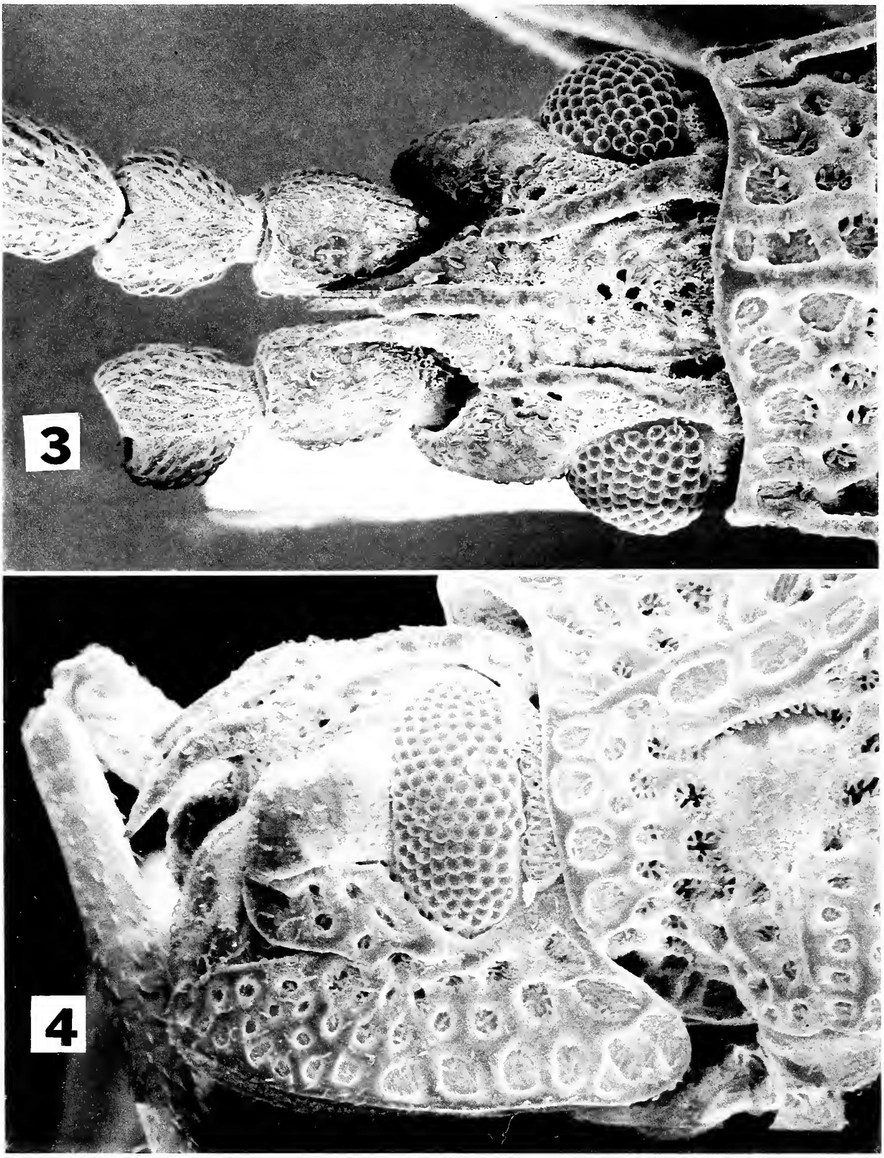
Figs. 1–4, 6, 7

Description. General coloration yellowish brown, with a few fuscous markings on hemelytra and sparsely set with short, appressed, thickened setae. Head quadrate, antennae set in front of eyes, antenniferous tubercle surrounding base of segment I, eyes red, proportionately large (compared to *infuscata*), crescent-shaped around side



Figs. 1, 2. Dorsal views of *Melanorhopala froeschneri*. 1. paratype male. 2. paratype female.

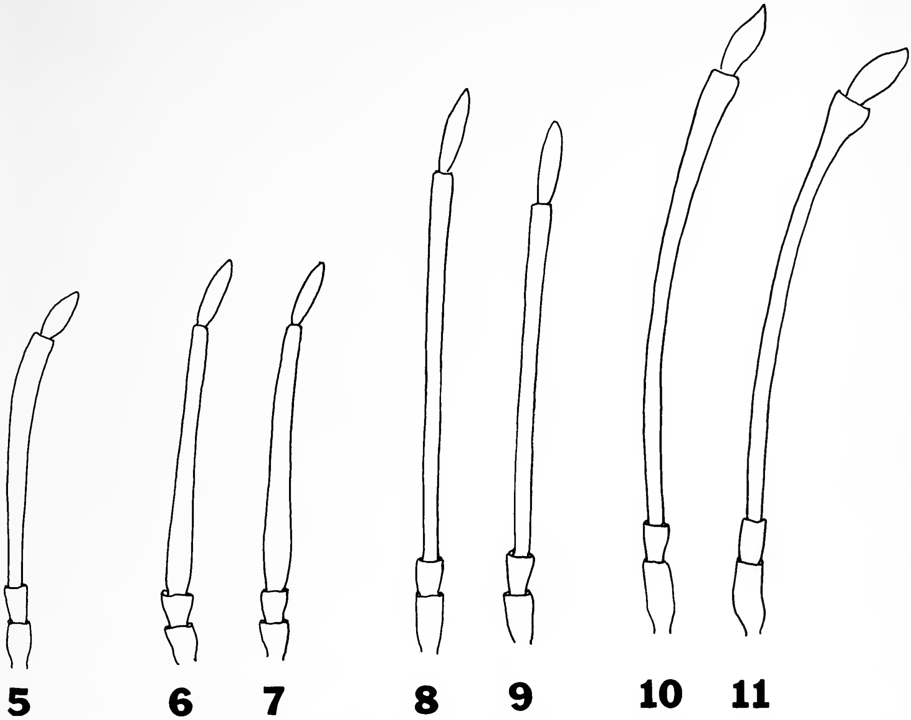
of head, higher than long, height from lateral aspect greater than distance from lower margin of eye to lower margin of buccula (Fig. 4); dorsum with 5 reclining spines (Fig. 3), 2 laterally, arising from posterior lobe, extending to bases of anterior spines, bases just covered by anterior margin of pronotum, mesal spine arising at level even with anterior margin of eyes, 2 forward spines arising at level with antennal bases, apices curving inward and around apex of mesal spine, forming a loose but rather thick-pointed process; vertex between lateral spines and posterior to mesal spine deeply punctate, with a few sericeous setae; buccula large, rectangular in lateral aspect, ventrally forming an elongate U-shaped margin around first rostral segment. Rostrum extending beyond metacoxae to posterior margin of 2nd abdominal segment. Antennae moderately thickened (Figs. 6, 7), closely set with appressed thickened setae, segments I and II barrel-shaped, subequal in length, segment III longest, distinctly thickened on basal half, tapering to apex, uniformly yellowish brown, becoming infuscated on some specimens (at least dead ones), segment IV fusiform, 2 or more times the length of I and II combined. Pronotum tricarinate (Figs. 1, 2), much longer than wide, widest at humeral angles, anterior lobe narrowest, width about equal to width of head across eyes, gradually widening to humeral angles of posterior lobe, basal process triangular, covering scutellar area. Hemelytra yellowish brown, areoles fuscous along inner margin of corium and middle of basal half and on either side of sutural or "membranal" area, subparallel in males (Fig. 1), slightly widened across middle, elongate oval in females (Fig. 2), apex subtruncate, broadly rounded, bra-



Figs. 3–4. *Melanorhopala froeschneri.* 3. Dorsal view of head (paratype male). 4. Lateral view of head with antennae removed (paratype female).

chypterous forms unknown, costal area with a single row of areoles on basal half. Ventral surface and legs yellowish brown, tarsi and claws fuscous.

Measurements (female in parentheses; all measurements in millimeters). Male length [head to apex of hemelytra] 4.24–4.60 (4.48–5.08), width across widest point



Figs. 5–11. Antennae of *Melanorhopala* spp. 5. *balli,* male. 6. *froeschneri,* male. 7. *froeschneri,* female. 8. *infuscata,* male. 9. *infuscata,* female. 10. *clavata,* male. 11. *clavata,* female.

of hemelytra 1.44–1.66 (1.80–1.88). Head width 0.60 [all specimens measured] (0.56–0.64). Antennae: Length of segment I 0.20–0.24 (0.22–0.24), width 0.16–0.18 (0.14–0.16); II 0.16–0.20 (0.16), width 0.16–0.18 (0.14–0.16); III 1.60–1.68 (1.46–1.60); basal width 0.16–0.18 (0.12–0.16), apical width 0.14 (0.12–0.16); IV 0.46–0.48 (0.42–0.48). Pronotal length 1.80–1.96 (1.92–2.04), humeral width 1.06–1.16 (1.12–1.16).

Holotype. ♂ USA. **Tennessee:** *Tipton Co.,* Covington, Rt 51, June 2, 1985, T. J. Henry (TJH) and A. G. Wheeler, Jr. (AGW) colls., taken on vines of trumpet creeper, *Campsis radicans* (L.) Seem.; deposited in the National Museum of Natural History, Washington, D.C. [USNM].

Paratypes. DELAWARE: 2♂♂, ♀, *Sussex Co.,* Trussum Pond, Jul. 10, 1982, on bark of *Taxodium distichum* (L.) L. C. Rich. [*C. radicans* vines present], AGW (Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg [BPI]). KENTUCKY: 7 ♂♂, 2 ♀♀, *Warren Co.,* Bowling Green, June 5, 1985; TJH and AGW, on *C. radicans* (BPI, USNM). MARYLAND: ♂, ♀, *Calvert Co.,* Rt. 4, Lusby, 20 Jul. 1985, TJH and AGW, on *C. radicans* (BPI, USNM); 2♂♂, 2 ♀♀, *Caroline Co.,* 4 Jul. 1985, TJH and K. Henderson-Henry, on *C. radicans* (USNM); 2 ♀♀, St. Mary's Co., Rt 4, Town Point, Jul. 20, 1985, TJH and AGW, on *C. radicans* (BPI, USNM); ♀, *St. Mary's Co.,* Point Lookout, Jul. 20, 1985, TJH and AGW on *C. radicans* (BPI, USNM); ♀, *Queen Annes Co.,* Church Hill, Jul. 27, 1985, on *C. radicans,* AGW (BPI).

NORTH CAROLINA: 6♂♂, 7 ♀♀, *Craven Co.,* New Bern, June 15, 1985, on *C. radicans* AGW (BPI); ♂, ♀, *Martin Co.,* Williamston, June 15, 1985, on *C. radicans,* AGW (BPI). TENNESSEE: 9♂♂, 7 ♀♀, same data as for holotype (BPI, USNM); 11♂♂, ♀, *Tipton Co.,* Rt 51, 3 mi N of Covington, June 2, 1985, TJH and AGW, on *C. radicans* (BPI, USNM).

Remarks. As shown in the key, *froeschneri* is most closely related to *infuscata* in the generally subparallel, macropterous (brachypterous forms are unknown) hemelytra that are subtruncate apically (Figs. 1, 2), the apically slender antennal segment III (Figs. 6–9), and the long rostrum. The unique male holotype of *balli* (indicated as a female in the original description) and most specimens of *clavata* are brachypterous, having the hemelytra acuminate and diverging apically. Macropterous individuals of the latter apparently are rare as only 3 or 4 fully winged specimens (out of more than 100) are in the USNM collection.

DESCRIPTION OF FIFTH INSTAR

Fig. 12

Description (in alcohol, N = 5). Pale yellowish brown, elongate oval, length 3.33–3.50. Head quadrate, antenniferous tubercles distinct, somewhat acute on outer ½ in dorsal aspect; armed with 5 erect spines, each spine set with tiny, setigerous tubercles, 2 basal spines longest, set on vertex at inner posterior margin of each eye, mesal spine at middle of frons, sometimes apically bifid, 2 anterior spines at base of tylus between antenniferous tubercles; Y-shaped epicranial suture distinct, pale. Rostrum length 1.75–1.76, extending to base of second abdominal segment, segment one set in gular groove, laterally margined by bucculae. Antennae: Segment I length 0.14–0.16, barrel-shaped; II 0.10–0.12, barrel-shaped; III 1.20–1.24, cylindrical, thickened on basal ½, tapering apically, some specimens infuscated on apical ½; IV 0.42–0.46, fusiform, fuscous. Pronotum trapeziform, concave, posterior margin broadly tapered to a distinct point, meson with a pale, narrow carina, area around calli transversely depressed, lateral margins with 2 erect spines, the posterior spine longest; wing pads elongate, broadly rounded and infuscated apically, lateral margin of each with 2 erect spines. Abdomen broadly rounded, concave with central ⅓ raised and rounded dorsally, raised area with 5 erect spines, 1 at middle of segment II and a pair on segments V and VI; laterally set with an erect spine at posterior angle of each segment, genital segment with 2 spines directed posteriorly. Venter uniformly pale yellowish brown, meson of abdomen with distinct keel; legs pale yellowish brown, unarmed, set with extremely fine, short setae.

NOTES ON HABITAT AND HOST

We have found *M. froeschneri* only on trumpet creeper, a deciduous, woody vine characterized by large, short-stalked, trumpet-shaped flowers and clinging, aerial rootlets. This bignoniaceous plant, native from New Jersey to Ohio, Florida, and Texas and hardy as far north as Massachusetts, is common in moist woods, on fencerows, and along roadsides. Used for covering tree stumps, masonry walls, and rock outcrops, *Campsis radicans* often escapes from cultivation and in the southern states may be a weed in cropland (Gleason, 1963; Everett, 1981).

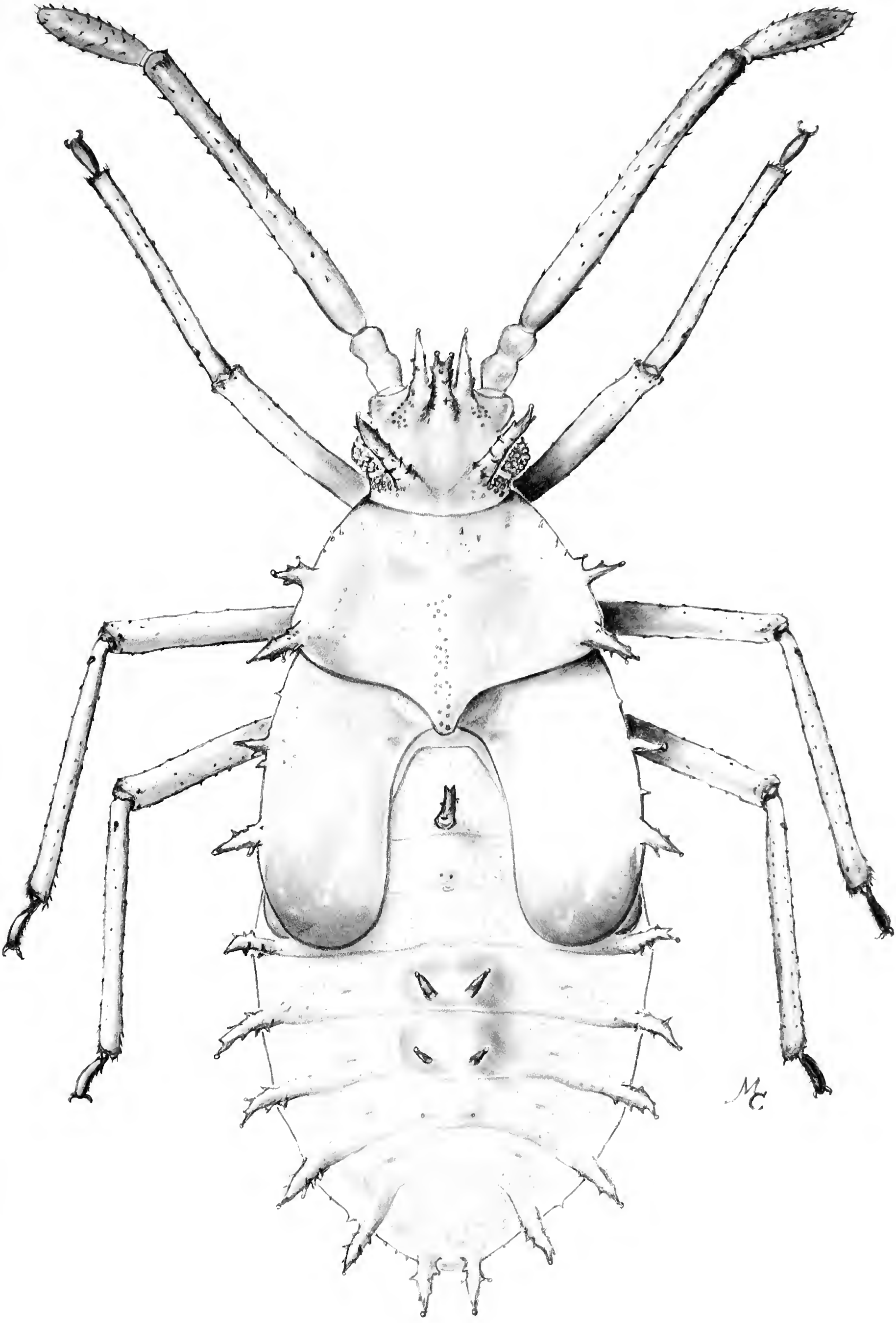


Fig. 12. Dorsal view of fifth-instar nymph.

Fig. 13. Typical habitat of *M. froeschneri,* showing trumpet creeper on tree trunk.

Melanorhopala froeschneri was collected on *C. radicans* growing mainly in shaded situations along hedge rows and woodland borders. Nymphs and adults were beaten from trumpet creeper attached to various deciduous trees and to conifers such as bald cypress and pine. We also detected populations by pulling vines away from tree trunks (Fig. 13) and observing the bugs crawling on trumpet creeper stems or scurrying for cover in bark crevices. They were associated with and appeared to feed only on the thicker, green stems (the latter also observed in rearing dishes) rather than on young stems or older, brown stems. Only in one locality did we find bugs on sprawling vines not attached to a tree. In this case, the unusually large size of the population on adjacent vines attached to a tree trunk appeared to account for this exception.

Colonization of *C. radicans* by *M. froeschneri* probably depends not on the "host" tree but on growth stage of the vine (populations were not observed on young vines) and on suitable conditions of humidity and other microenvironmental factors provided by the vines and "host" tree. On one occasion we observed black excrement on a trumpet creeper leaflet but, unlike most tingids, *M. froeschneri* does not colonize and feed on (at least to any extent) the abaxial surface of host foliage. Our collection of mainly late instars and teneral adults in Kentucky and Tennessee in early June, adults and only an occasional late instar in North Carolina and Virginia in mid-June, and adults only in Delaware and Maryland during July suggests that this lace bug has a univoltine life cycle.

Even though *M. froeschneri* may be abundant on trumpet creeper (more than 50 or 100 individuals on a vine), the cryptic, stem-feeding habits of this lace bug nearly preclude its detection by usual collecting methods. In general, *Melanorhopala* spp. are poorly represented in collections, and the habits of these bugs are little known. In the Washington, D.C., area *M. infuscata* has been taken on bark and at sap of tulip tree, *Liriodendron tulipifera* L. (Parshley, 1917, 1920), and on flowers of New Jersey tea, *Ceanothus americanus* L. (McAtee, 1923). Parshley (1920) suggested that *M. infuscata* lives on the bark of tulip tree, where it perhaps subsists "on sap from the trunk rather than from the leaves." An alternative hypothesis is that this species develops on stems of some vining plant attached to *Lirodendron* and other trees. The possibility that certain *Melanorhopala* spp. feed on vines and that *M. clavata* is associated with stems of its apparent host, goldenrod (Bailey, 1951; Slater and Baranowski, 1978), deserves consideration.

ACKNOWLEDGMENTS

We thank R. T. Schuh (AMNH) and K. Valley (BPI) for reviewing the manuscript. Ms. M. L. Cooley illustrated the fifth instar and R. L. Friedman helped with the electron micrographs (both of the Syst. Entomol. Lab., Agric. Res. Serv., USDA, % USNM).

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J. New York Entomol. Soc. 94(2):245–248, 1986

FROESCHNEROCADER DENTICOLLIS (HETEROPTERA: TINGIDAE): A NEW GENUS AND SPECIES OF CANTACADERINAE FROM BORNEO

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Abstract.—Froeschnerocader denticollis, new genus and new species, is described from Borneo, Eastern Malaysia.

The following description is furnished to provide a name to be included in a forthcoming list of Tingidae collected in 1983 on Borneo and Palawan Islands by Dr. Bernd Hauser, Musée d'Histoire Naturelle de Genève. The primitive subfamily Cantacaderinae, apart from some *Cantacader* spp., is represented in this material by a unique but very distinct specimen, representing a new genus and species. I am very pleased to name the genus in honor of Dr. Richard C. Froeschner, as an acknowledgement of his valuable contributions to the study of this subfamily on a worldwide level and a personal appreciation and mark of friendship.

Froeschnerocader, new genus

Diagnosis. This genus, belonging to the tribe *Cantacaderini* (see Drake, 1960; Froeschner, 1968), differs from all other known genera of the tribe (*Cantacader* Amyot and Serville, *Ceratocader* Drake, *Nectocader* Drake, and *Teratocader* Drake) in having the bucculae hardly surpassing the tip of clypeus. Furthermore, the absence of hemelytral shoulders and the presence of toothlike projections on the paranota distinguish it from *Nectocader* and *Teratocader.* Its pronotal structure resembles that of *Ceratocader,* but in the latter, the scutellum is not covered; *Ceratocader* also has more than one transverse vein on the discoidal area.

Description. Very minutely reticulate above. Head armed dorsally with two pairs of spiniform processes. Bucculae hardly surpassing tip of clypeus, not closing buccal sulcus. Antennae slender.

Pronotum roughly semicircular posteriorly, covering the scutellum but not the hemelytral clavus. Paranota slightly raised, with several toothlike projections. Hood triangular, its tip protruding above the front. Disc bearing 5 carinae, median carina continuing on hood, two mediolateral carinae crossing entire disc, two external ones abbreviated.

Hemelytra without shoulders. Stenocostal areas complete, uniseriate. Costal laminae very broad, vein (R + M) very prominent. Discoidal areas crossed transversely on posterior by a secondary vein. Legs relatively stout, all femora bearing an external spur apically above their apex. Rostral furrow open behind. Metathoracic scent grooves clearly visible.

Type species. Froeschnerocader denticollis, new species.

Froeschnerocader denticollis, new species
Figs. 1–6

Description. Based upon a unique macropterous male. Habitus, Figure 1; lateral view of anterior half, Figure 4; ventral side, Figure 5. Body subglabrous. Dorsum brownish yellow, mottled with whitish areas; pronotal disc and head whitish; antennae pale brownish yellow, except apical half of 4th segment black; legs pale brownish yellow; tips of tarsi darkened.

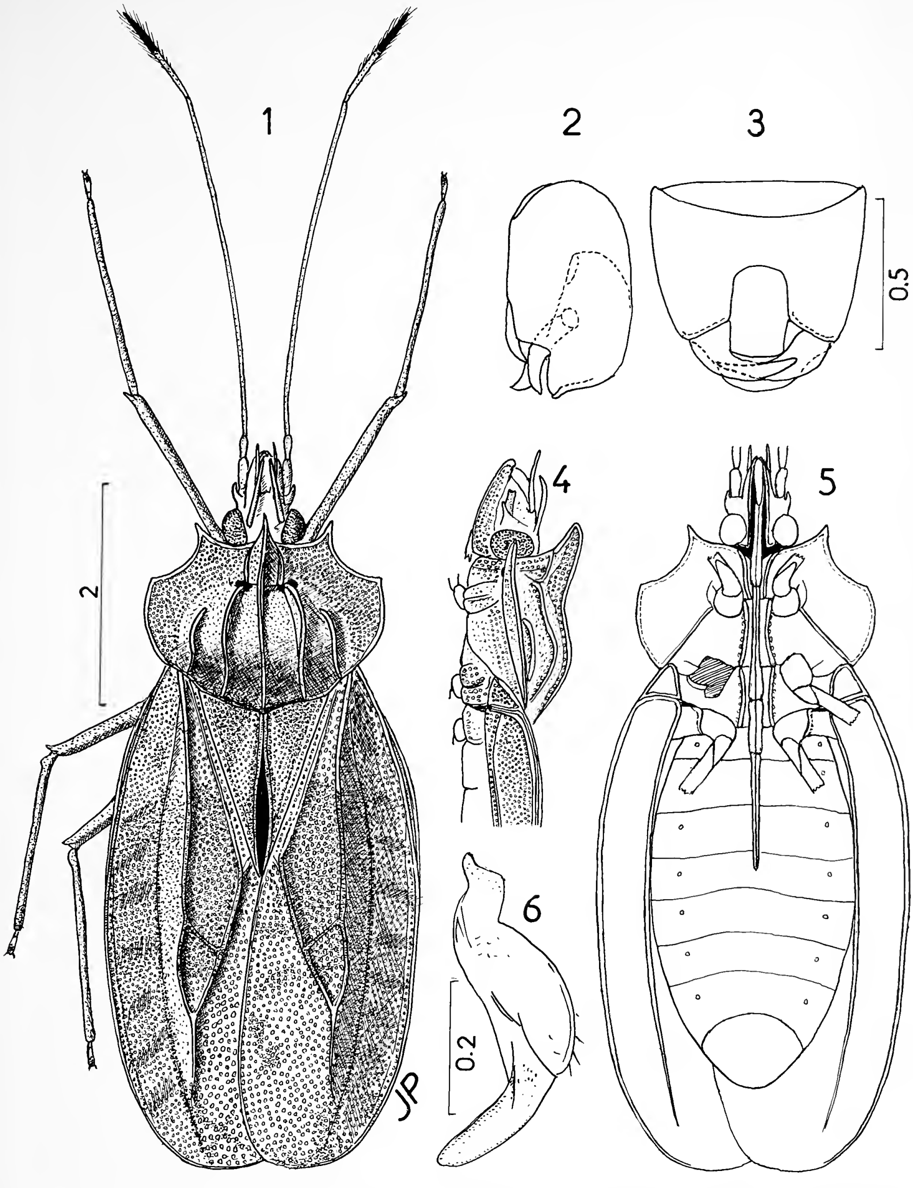
Head relatively short. Eyes (as seen from above) large, convex, with internal edges strongly diverging, 1.1 times broader than front at narrowest point between them. Posterior pair of spiniform processes near middle of internal edge of eyes, anterior pair near anterior edge of front, both pairs of processes thin, slightly arched, pointing anteriorly, as long as antennal segments I + II. Antenniferous tubercles acute, small, arched inward. First antennal segment hardly as long as eyes, almost cylindrical, attenuated at base; 2nd segment a little shorter, attenuated at both ends; 3rd segment slender, cylindrical, almost 4 times longer than width across eyes, and more than 4 times longer than spindle-like 4th segment. Bucculae (Fig. 4) narrowing from base to apex, hardly surpassing clypeus. Rostrum reaching posterior edge of sternite V (apparent IV).

Pronotum 1.25 times broader than long. Paranota horizontal, not clearly separated from disc, bearing 6–8 rows of small areolae; sides broadly arched on posterior half, forming two angular projections on anterior half, the most anterior spinelike at apex. Hood forming an elongate triangle, its tip protruding above the front; hood bounded laterally by two small carinae almost continuing the mediolateral carinae on disc. Disc convex, densely and finely punctate. Median carina narrow, bearing only one row of small areolae on disc, then broadening to 5–7 rows at base of the hood and continuing with several rows on the hood. Mediolateral carinae bisinuate on posterior half of disc, shortly curved inside before ending at transverse sulcus limiting base of the hood. External carinae bisinuate, converging anteriorly, ending onto anterior third of disc.

Hemelytra 1.6 times longer than broad; anterior angles absent; sides slightly arched, with maximum breadth near middle. Clavus forming elongate triangles, with 8 rows of areolae at broadest point. Stenocostal areas uniseriate, slightly reflexed above in anterior part. Costal laminae broad, raised (mainly anteriorly), bearing slight, irregular, transverse swellings; 9 rows of areolae at broadest point. Subcostal areas concave, with 5 rows of areolae, overhung by very prominent (R + M) vein. Discoidal areas elongate, attaining ⅔ of hemelytral length, bearing about 10 rows of areolae at widest point; one transverse auxiliary vein crossing them apically, forming small triangular cell. Partially overlapping sutural areas rounded apically with about 13–14 rows of areolae at widest point.

Legs rather stout, protibiae 2.15 times longer than width across eyes; meso- and metatibiae about same length as protibiae. Tarsi relatively short. Rostral sulcus deep, about same breadth on meso- and metasternum. Meso- and metasternal laminae slightly arched, their convex side turned towards the sulcus. Pygophore, Figures 2 and 3; paramere, Figure 6.

Measurements (in mm): Length: head 0.81; pronotum 1.76; hemelytra: 4.70; an-



Figs. 1–6. *Froeschnerocader denticollis.* 1. Habitus. 2. Pygophore (profile). 3. Pygophore (from above). 4. Anterior half of body (profile). 5. Ventral side of body. 6. Paramere. Scales in mm.

tennal segments: (I) 0.28, (II) 0.25, (III) 3.10; (IV) 0.75; protibia 1.75; profemora 1.78; total length from tip of clypeus to apex of hemelytra 6.50. Breadth: head, width across eyes 0.85, front (at narrowest point) 0.25; pronotum 2.15; hemelytra 2.87.

Holotype. ♂ EASTERN MALAYSIA: **Sabah,** northern Borneo, Mt. Kinabalu National Park, Poring Hot Springs, alt. 500 m, 21 III 1983, taken beating trees and shrubs around pools, C. Lienhard collector; preserved in the collection of the Musée d'Histoire Naturelle de Genève, Switzerland.

I am indebted to Bernd Hauser for sending his material, the main part of which is being considered in another paper.

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J. New York Entomol. Soc. 94(2):249–261, 1986

TWO NEW GENERA AND SEVEN NEW SPECIES OF ARADIDAE (HETEROPTERA)

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Abstract.—The following new taxa are described: *Aphyseteres nasutus.* (Malaysia, Borneo); *Calisius borneensis* (Malaysia, Borneo); *Dimorphacantha borneensis,* (Malaysia, Borneo); *Froeschnerissa,* new genus for *Froeschnerissa heveli* (Malaysia, Borneo); *Glochocoris borneensis* (Malaysia, Borneo); *Heissia* new genus for *Heissia rotundata* (Nigeria), and *Notapictinus dollingi* (Costa Rica). The species *Calisius stappersi* Schouteden and its "var.?" are transferred to the genus *Heissia* as its second species. A key is given to separate the six known genera of *Calisiinae.*

I have had the privilege of studying a small but highly interesting lot of Aradidae through the kindness of the following individuals: H. M. André and G. Schmitz, Musée Royal d'Afrique Central, Tervuren, Belgium; W. R. Dolling, British Musem (Natural History), London, England; J. P. Duffels, Instituut voor Taxonomische Zoologie, Universitet van Amsterdam, Amsterdam, The Netherlands; Ernst Heiss, Innsbruck, Austria; and Gary P. Hevel, National Museum of Natural History, Smithsonian Institution, Washington, D.C. To these persons I express my sincere gratitude.

The two new genera, 7 new species and 1 new combination proposed herein pertain to the subfamilies Calisiinae, Carventinae, and Mezirinae.

All measurements were taken with a micrometer eyepiece, 25 units = 1 mm. In ratios the first figure represents the length and the second the width of the part measured. All measurements are in millimeters.

SUBFAMILY CALISIINAE

The subfamily Calisiinae is one of the oldest among Aradidae. In two genera, *Paracalisiopsis* Kormilev, 1963, and *Paracalisius* Kormilev, 1974, connexivum I is fully developed but in other genera of Calisiinae it is reduced to a triangular sclerite superimposed on connexivum II anteriorly. In the new genus *Heissia* connexivum VIII (♀) is fully developed, a character unique among the Aradidae.

KEY TO THE GENERA OF CALISIINAE

1. Antenna simple, first three segments subequal in length, IV longer but without dispersed dots 2
– Antenna with first three segments moniliform, IV much longer and with dispersed dots 3
2. External borders of connexivum with a double row of granules; connexivum VIII absent .... *Calisius* Stål
– External borders of connexiva with granules in upper row and spicules in lower row; connexivum VIII present (♀) .... *Heissia,* new genus
3. Connexivum I triangular, placed in front of connexivum II 4

- Connexivum I reduced to small triangular sclerite superimposed on Connexivum II anteriorly 5
4. Exterior borders of connexiva with a double row of granules. ..... *Paracalisius* Kormilev
- Exterior borders of connexiva with a single row of flat teeth .... *Paracalisiopsis* Kormilev
5. Pronotum trapezoidal, not constricted laterally; stridulatory apparatus absent .... *Calisiopsis* Champion
- Pronotum constricted laterally, forming two lobes; stridulatory apparatus present along outer posterior margin of metapleuron .... *Aradacanthia* Costa

Calisius Stål, 1860

Calisius borneensis, new species

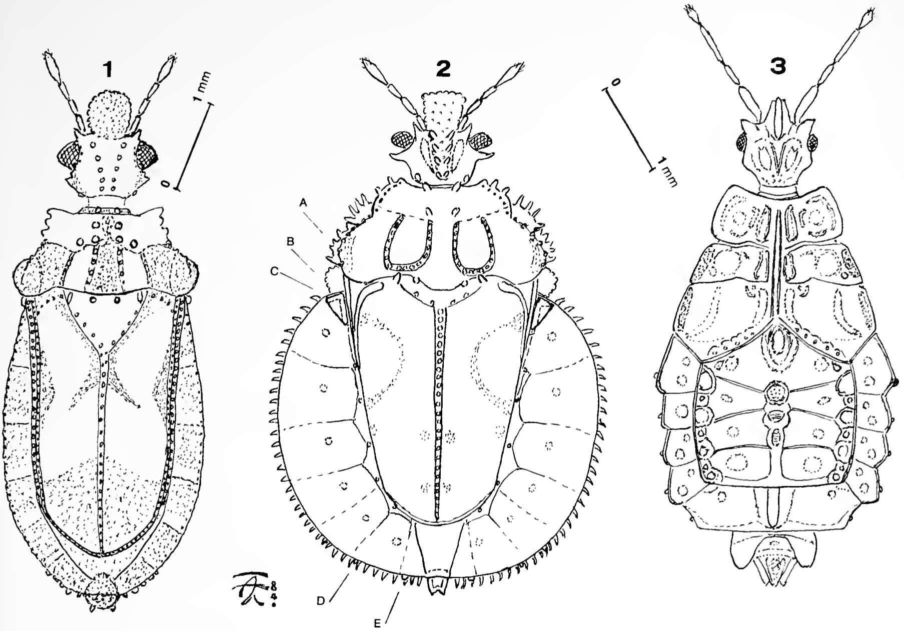
Fig. 1

Diagnosis. Calisium borneensis is related to *C. ashlocki* Kormilev from New Guinea, but differs in having the basal triangular elevation of scutellum with 2 (1 + 1) spicules and 2 (1 + 1) small granules between them; scutellar carina granulate along entire length; and lateral borders of scutellum and visible portion of corium granulate.

Description. Male. Ovate; head, pronotum, scutellum and connexivum, granulate. HEAD: almost as long as width across eyes (14:15); anterior process ovoid, rounded anteriorly, convex laterally and granulate, reaching ½ of antennal segment III; antenniferous tubercles short, blunt, directed slightly downward; vertex with a double row of granules converging backward. Antennae short and thin, shorter than width of head (12.5:15); relative length of antennal segments I to IV are: 2.5:2.5:2.5:5. Labium extending to hind border of labial groove, which is closed posteriorly. PRONOTUM: trapezoidal, half as long as maximum width (12:25); lateral borders with a row of granules, 6 (3 + 3) on fore lobe and 4 (2 + 2) on hind lobe; middle carinae high, parallel, roughly granulate on fore lobe, less roughly on hind lobe; lateral carinae finely granulate, diverging on hind lobe. Fore disc very coarse on fore lobe, hind disc punctured between carinae. SCUTELLUM: less than twice as long as width at basal ⅓ (35:20); basal triangular elevation with 2 (1 + 1) spicules anteriorly and with 2 (1 + 1) small granules between them; lateral borders of elevation and median carina granulate. Lateral borders of scutellum densely granulate along entire length. HEMELYTRA: corium appearing as a granulate carina laterad of scutellum reaching hind border of connexivum V. ABDOMEN: ovate, slightly longer (length of abdomen measured on ventral side) than its maxiumum width (28:26). Exterior borders of connexiva granulate; disc bicolored: black and yellow brown. Paratergites of VIII small, appearing bicuspidate because of granules. Hypopygium globose (7.5:12). Sternum VII with median depression. Spiracles II to VI ventral, VII and VIII lateral and visible from above. LEGS: trochanters free. COLOR: head black, vertex and antennae brown; pronotum red brown, black medially between inner carinae and outside of external carine; scutellum black on triangular elevation; 2 (1 + 1) sublateral elongate spots in middle and apical ⅓ of disc, yellow brown; 2 (1 + 1) connecting elongate spots behind triangular elevation brown; trochanters yellow, femora and tibiae brown.

Measurements: Total length 2.80; width of pronotum 1.00; width of abdomen 1.04.

Holotype. ♂ MALAYSIA, Borneo, Sabah: 1 km S of Kundasang, 1,530 m, Aug. 24, 1983, G. F. Hevel and W. E. Steiner; deposited at the National Museum of Natural History, Washington, D.C.



Figs. 1–3. 1. *Calisius borneensis,* ♂, dorsal aspect. 2. *Heissia rotundata,* ♀, dorsal aspect. A—carina of the propleuron; B—metapleuron; C—connexivum I superimposed on II; D—spiracle of connexivum VII; E—spiracle of connexivum VIII. 3. *Frosechnerissa heveli,* ♀, dorsal aspect.

Heissia, new genus

Diagnosis. Heissia can be separated from other genera of Calisiinae by the fully developed connexivum VIII in the females; males are unknown.

Description. Female. Head, pronotum, scutellum, and exterior borders of connexivum with rows of granules or spicules; hind lobe of pronotum and disc of scutellum with rough punctures. HEAD: shorter than width across eyes; anterior process subtruncate anteriorly, its lateral borders converging backward, reaching tip of antennal segment II; antenniferous tubercles small, diverging; postocular long, slightly produced beyond outer border of eyes. Antennae short, shorter than width of head across eyes; first three antennal segments subequal in length, IV twice as long as III. Labium reaching hind border of labial groove, which is closed posteriorly. PRONOTUM: subtrapezoidal, less than half as long as maximum width; fore lobe much narrower than hind lobe; collar truncate; lateral borders of fore lobe with 4 (2 + 2) long spicules and a row of small granules above; lateral borders of hind lobe very convex, with a row of spicules, and above a row of granules in continuation of the rows of fore lobe; hind border roundly produced backward medially and twice sinuate sublaterally. Fore disc with 2 (1 + 1) long spicules behind collar and overhanging it; 2 (1 + 1) long spicules behind them at the hind border of fore lobe; 2 (1 + 1) large loops, formed by rows of semifused granules on hind disc. SCUTELLUM: longer than maximum width at base; lateral borders straight, converging backward, apex rounded; triangular elevation at base from which arises median carina; 2 (1 + 1) large granules at front and laterad with 2 (1 + 1) large spicules overhanging hind border of pronotum; lateral borders of triangular elevation with a few large granules. Median carina with a row of large granules; lateral borders of scutellum carinate at base, then with a row of obscure granules, evanescent at ⅔ of scutellum; disc densely, roughly punctured. HEMELYTRA: almost completely covered by scutellum, exterior border of corium visible at basal angle of scutellum and then produced backward as a carina until $^3/_5$ of scutellum. ABDOMEN: almost round, slightly shorter than maximum width across segment III; narrow portion of disc and a very wide connexivum appearing laterad of scutellum; segments of connexiva semifused, their limits obscured; reduced segment I superimposed on segment II anteriorly; each segment from II to VII bearing round callous spot in middle. Fully developed connexivum VIII placed between connexivum VII and tergum VIII in female, which is unique in Aradidae. Spiracles very small; II ventral, placed nearer to border; III to VI ventral, placed far from border; VII and VIII lateral, visible from above. Exterior borders of connexiva II to VIII with a double row of granules (upper row), and spicules (lower row). Ventral side: propleuron with a high, denticulate carina medially, partially visible from above. Meso- and metapleura granulate. Pro- and mesosternum slightly depressed medially; metasternum flat, with hind border deeply and roundly cut out medially, forming 2 (1 + 1) large, rounded promontories laterad of median sinus. Hind borders of sterna III to VI angularly cut out medially. LEGS: trochanters free; femora fusiform, unarmed; fore tibiae with a small comb subapically; claws with arolia.

Type species. Heissia rotundata, new species.

Etymology. Heissia, new genus, named in honor of my friend Ernst Heiss.

Heissia rotundata, new species

Fig. 2

Description. Female. Ratios: head 25:29; relative length of antennal segments I to IV: 5:5.5:5:10; pronotum 25:63; fore lobe to hind lobe of pronotum 38:63; scutellum 65:50; abdomen 80:87. COLOR: head, fore lobe of pronotum and connexivum, orange, the latter with red exterior borders; hind lobe of pronotum and scutellum ivory with some brown spots. Ventral side orange; venter pale medially.

Measurements: Total length 5.40; width of pronotum 2.52; width of abdomen 3.48.

Holotype. ♀ NIGERIA, Udo Fr. M State W, 11.IV.1975, J. T. Medler, deposited at the Heiss collection, Innsbruck, Austria.

Heissia stappersi (Schouteden), **New Combination**

Calisius stappersi Schouteden, 1919, 7:65.

Diagnosis. Female. Similar to *Heissia rotundata* but longer and narrower, ratio length:width of the body 1.60:1 (in *H. rotundata* 1.55:1); abdomen more ovate, as long as maximum width, ratio 95:95 (in *H. rotundata* shorter than wide 80:87); anterior process of head rounded anteriorly (in *H. rotundata* subtruncate). Color more reddish brown, with hind lobe of pronotum and scutellum almost white with reddish-brown spots. Ratios: Head 30:33; relative length of antennal segments I to IV are: 6:6.5:5.5:10; pronotum 32:65; scutellum 72:55; abdomen 95:95.

Measurements: Total length 6.08; width of pronotum 2.60; width of abdomen 3.80.

Calisius stappersi var.? belongs to the same species; it is only slightly larger, but of the same color.

Ratios: Head 33:34; relative length of antennal segments I to IV are: 5.5:7:5.5:10; pronotum 33:65; scutellum 73:57; abdomen 96:95.

Specimens examined. ♀, (Belgian Congo) ZAIRE, Petite Plaine de Tembwe; 23.VI.1912, Dr. Stappers; holotype of Schouteden, deposited in the Musée Royal d'Afrique Centrale, Tervuren, Belgium. ♀, ZAIRE, Albertville, Fine I.1933, L. Burgeon, "*Calisius stappersi* var.?"; deposited in Tervuren.

SUBFAMILY CARVENTINAE

Froeschnerissa, new genus

Diagnosis. Froeschnerissa is related to *Kolpodaptera* Usinger and Matsuda, 1959, but may be separated from it by the pentagonal central dorsal plate (subrectangular in *Kolpodaptera*), by the dorsum mostly covered by maze of tiny, irregular carinae and punctures and by posteroexterior angles of connexivum VII not produced backward.

Description. Apterous, covered with light brown incrustation; dorsum with a mesh of tiny, irregular carinae and punctures. HEAD: longer than width across eyes; anterior process tricuspidate, clypeus slightly longer than jugae, slightly shorter than half of antennal segment I; antenniferous tubercles slightly declivous; postocular borders slightly inflated behind eyes, then straight and converging, without tubercles; eyes small, deeply inserted into head. Antennae short, less than twice as long as width of head; antennal segment I as long as III and II as long as IV. Labium preapical, arising from splitlike atrium, not reaching hind border of labial groove, which is closed posteriorly. PRONOTUM: less than half as long as maximum width; collar distinct; anterolateral angles angularly rounded anteriorly and inflated on disc; lateral borders straight, diverging backward. Disc narrowly depressed medially, with narrow, double carina in the depression continuing posteriorly across meso- and metanotum and terga I and II until central dorsal plate. Pronotum separated from mesonotum, laterad of median carina, by 2 (1 + 1) oblique sulci. MESONOTUM: shorter and wider than pronotum; median carina flanked by 2 (1 + 1) longitudinal, glabrous elevations and further laterad with a maze of tiny, irregular carinae and punctures. Lateral borders convex, raised exteriorly. Mesonotum separated from metanotum, laterad of median carina, by 2 (1 + 1) deep, curved sulci. METANOTUM: shorter and wider than mesonotum, fused posteriorly with terga I and II. Disc longitudinally raised sublaterally. ABDOMEN: ovate, longer than maximum width across segment III, divided into three plates: first plate consisting of terga I and II fused with metanotum; second plate (=central dorsal plate), consisting of terga III to VI, and third plate of tergum VII. All three plates separated from each other, second plate also from connexivum, by deep sulci. Central dorsal plate raised medially on tergum III forming a high elevation in the shape of a rhomb; laterad of rhomb tergum III with 2 (1 + 1) round callous spots; tergum IV with 2 (1 + 1) subtriangular depressions, limited by carinae and further laterad with 4 (2 + 2) round callous spots; posteriorly near hind border, medially, small round depression, surrounded by carinae and with a few granules on disc. Tergum V sloping backward, with two scent gland scars medially, laterad of scars with 2 (1 + 1) transverse depressions, with discs covered with maze of tiny carinae and punctures; 2 (1 + 1) round callous spots in the middle of these depressions and 4 (2 + 2) round callous spots further laterad. Tergum VI with double median carina flanked by 2 (1 + 1) subtriangluar depressions and further laterad by 4 (2 + 2) round callous spots. Tergum VII is raised and carinate medially. Connexiva II and III fused, other separated by thin sulci. Each connexivum with 2 round callous spots. Exterior borders of connexivum finely carinate. Tergum VIII (♀) semicircular, transversely sulcate, paratergites conical, reaching ½ of tricuspidate segment IX. Spiracles II ventral, placed far from margin, III to VII lateral, visible from above, VIII ventral, not visible from above. Pro-, meso- and metasternum flat and smooth medially, Pleurae rugose. LEGS: trochanters fused with femora; fore tibiae with a small comb; claws with arolia.

Type species. Froeschnerissa heveli, new species.

Etymology. This new genus is named in honor of my friend, Richard C. Froeschner, for his seventieth birthday.

Froeschnerissa heveli, new species

Fig. 3

Description. Female. Elongate ovate, narrowing anteriorly. Ratios: head 24:22; relative length of antennal segments 12:7:12:7.5; pronotum 15:35; mesonotum 10:47; metanotum 5:56; abdomen 77:68; width of tergum VIII 15. COLOR: brown to dark brown, covered by light brown incrustation.

Measurements: Total length 5.32; width of pronotum 1.40; width of abdomen 2.72.

Holotype. ♀ MALAYSIA, Borneo, Sabah, Kinabalu National Park, summit trail, Pak Cave to Panar Laban, 3,200–3,500 m; 16.IX.1983. G. & J. Hevel and W. Steiner; deposited at the National Museum of Natural History, Washington, D.C.

Paratype. ♀, collected with holotype; deposited in the Kormilev collection.

Etymology. The species is named for its collector Gary F. Hevel of the Smithsonian Insitution.

SUBFAMILY MEZIRINAE

Aphyseteres Usinger and Matsuda, 1959

Aphyseteres nasutus, new species

Fig. 4

Diagnosis. Aphyseteres nasutus can be separated from *A. borneensis* Usinger and Matsuda, 1959, by the extremely long and tapering anterior process of head.

Description. Male. Ovate, apterous covered with dense, brown tomentum. HEAD: longer than width across eyes (100:67); anterior process very long, tapering, tip incised, reaching ½ of antennal semgment I; antenniferous tubercles short, blunt. Eyes semiglobose, placed in middle of front half of head; postocular borders straight, converging backward, without postocular tubercles. Vertex raised, elevation forked around base of clypeus. Antennae stout and long, 2.3 times as long as width of head

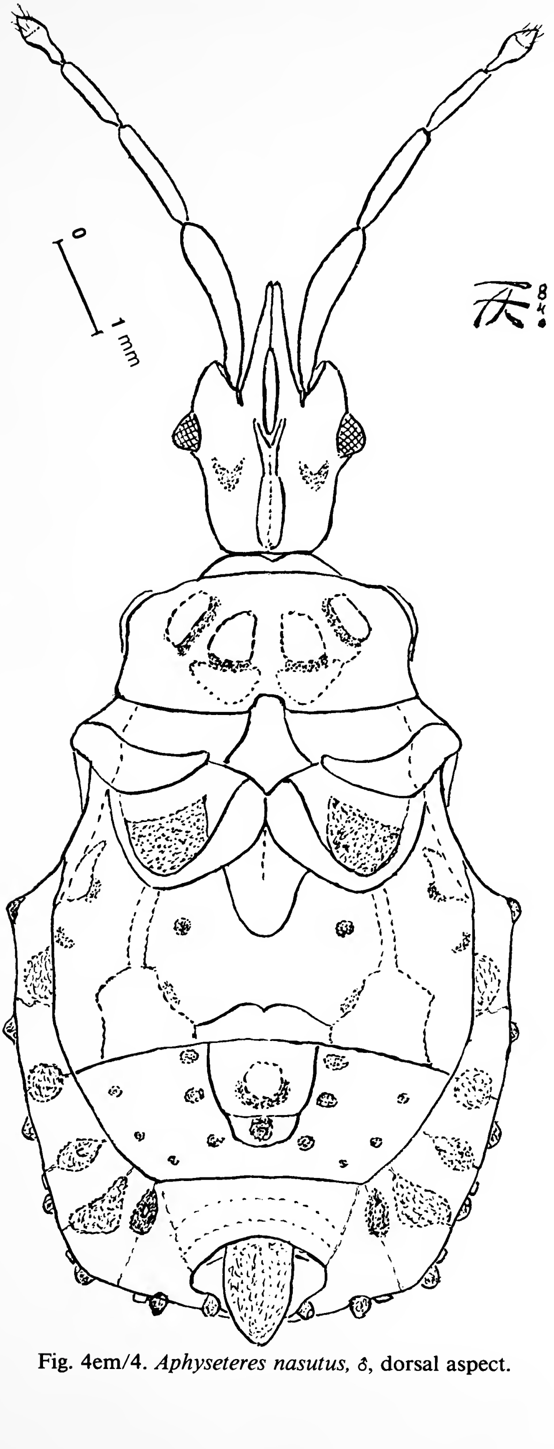


Fig. 4em/4. *Aphyseteres nasutus,* ♂, dorsal aspect.

across eyes; relative length of antennal segments I to IV 60:43:28:22. Labium arising from splitlike atrium, not reaching hind border of labial groove, which is open posteriorly. PRONOTUM: short and wide (50:108); collar slightly incised in middle; disc with 2 (1 + 1) large and high, ovate ridges, flanked by 2 (1 + 1) small and thin ridges; 2 (1 + 1) curved, transverse ridges behind large ridges, separated from each other by a depression., Hind border of pronotum convex laterally, sinuate medially. MESONOTUM: short and wide (20:136), elevated medially, elevation flanked by 2 (1 + 1) depressions, with 2 (1 + 1) high tubercles above scent gland openings. Mesonotum separated from metanotum by thin, transverse sulcus. Metanotum split by tergum I into 2 (1 + 1) semicircular plates connected laterally with lateral tubercles of mesonotum. ABDOMEN: longer than maximum width across segment II (193: 183). Tergum I small heart-shaped, separated from tergum II by 2 (1 + 1) thin oblique sulci. Tergum II large, strongly raised medially, with a thin median sulcus, flanked by 2 (1 + 1) oblique ridges; laterad of ridges with 2 (1 + 1) large, crescent-shaped, smooth, black spots, surrounded posteriorly by semicircular ridge, extending from oblique ridges. Tergum III strongly raised medially (highest point of abdomen), sloping laterally, with 2 (1 + 1) short, longitudinal, sublateral ridges. Tergum IV flat, lower medially than media elevation of tergum III, but strongly raised into 2 (1 + 1) high ridges sublaterally. Tergum V with high elevation medially, bearing traces of scent glands, strongly sloping laterally, external portion flat and low. Tergum VI strongly sloping medially from media elevation of tergum V, flat and low laterally. Central dorsal plate (terga II to VI) separated from connexivum and tergum VII by deep sulci. Tergum VII strongly raised medially for the reception of hypopygium, sloping laterally toward connexivum. Paratergites of VIII small, tuberclelike, with large, lateral spiracle. Hypopygium large (39:45), with strong median ridge overhanging hind border posteriorly. Connexivum II produced forward, touching upper end of metathoracic scent gland opening. Connexiva III to VII raised on posterior half, with salient tubercle on anterior half laterally. Spiracle II not visible; III to IV ventral, placed far from border, V to VII sublateral, slightly visible from above; VIII lateral. LEGS: long, unarmed; smooth, ovate spot in front of hind acetabula; femora cylindrical, slightly enlarged apically; front tibiae with white comb subapically; tarsi short; claws without arolia. COLOR: black, but most of body covered with dense, brown tomentum; apical half of antennal segment IV and claws yellow brown; eyes white with yellow tinge.

Measurements: Total length 14.52; width of pronotum 4.32; width of abdomen 7.32.

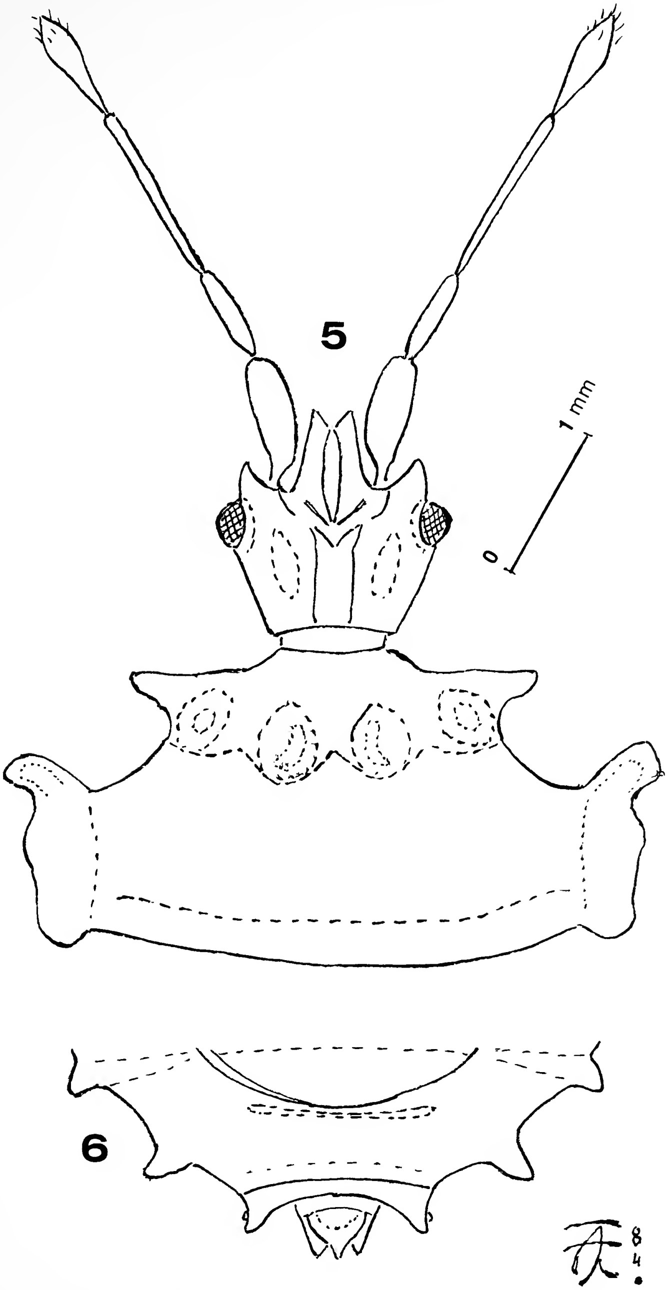
Holotype. ♂ C. BORNEO, Mt. Tibang, 1,500 m, 1925, Mjoberg coll., Dr. D. Mac Gillavry collection; deposited at the Amsterdam Museum of Natural History.

Dimorphacantha Usinger and Matsuda, 1959

Dimorphacantha borneensis, new species

Figs. 5, 6

Diagnosis. Previously *Dimorphacantha* had five species, two of which were brachypterous. The sixth species *D. borneensis,* is related to *D. distincta* Usinger and Matsuda, 1959, from Borneo, but is larger, the relative length of antennal segments is different, segment II is as long as IV, and the pronotal spines are more produced.



Figs. 5, 6. 5. *Dimorphacantha borneensis*, ♀. Head and pronotum. 6. Apex of abdomen from above.

Description. Female. Elongate ovate, granulate. HEAD: slightly shorter than width across eyes (35:37); anterior process cleft, jugae acute, longer than clypeus, reaching ½ of antennal segment I; antenniferous tubercles acute, parallel; postocular borders straight, converging backward, without tubercles. Vertex with 2 (1 + 1) thin, parallel ridges. Antennae stout, more than twice as long as width of head across eyes (83:37); relative length of antennal segments I to IV 23:15:30:15. Labium not reaching hind border of labial groove, which is closed posteriorly. PRONOTUM: less than half as long as maximum width across posterior spines (50:108); fore lobe narrower than hind lobe (67:108); fore disc sulcate medially, with 4 (2 + 2) semiobliterated ridges; hind disc dispersely granulate. Fore disc with 2 (1 + 1) long, blunt processes, directed somewhat obliquely sideways; hind disc with similar, but stronger and longer processes. SCUTELLUM: shorter than basal width (50:60); lateral borders sinuate, tip rounded; disc with sharp, narrow median ridge, transversely rugose laterad of it. HEMELYTRA: reaching ⅔ of tergum VII; corium reaching hind border of connexivum II, its apical angle blunt, apical border sinuate; membrane with anastomosed veins. ABDOMEN: ovate, shorter than maximum width across segment IV (96:112); lateral borders evenly rounded; posteroexterior angles of connexiva II to VI produced as blunt spines; VII larger than others and directed obliquely sideways. Spiracles II to VII ventral, not visible from above; VIII ventrolateral, slightly visible from above. Paratergites of VIII angular, reaching half of tricuspidate segments IX. LEGS: all femora with strong subapical spines. COLOR: black, apical half of antennal segment IV brown.

Measurements: Total length 8.80; width of pronotum 4.40; width of abdomen 4.48.

Holotype. ♀ MALAYSIA, Borneo, Sabah: Kinabalu National Park, Headquarters Area, 1,560 m; 6.IX.1983; G. F. Hevel and W. E. Steiner; deposited at the National Museum of Natural History, Washington, D.C.

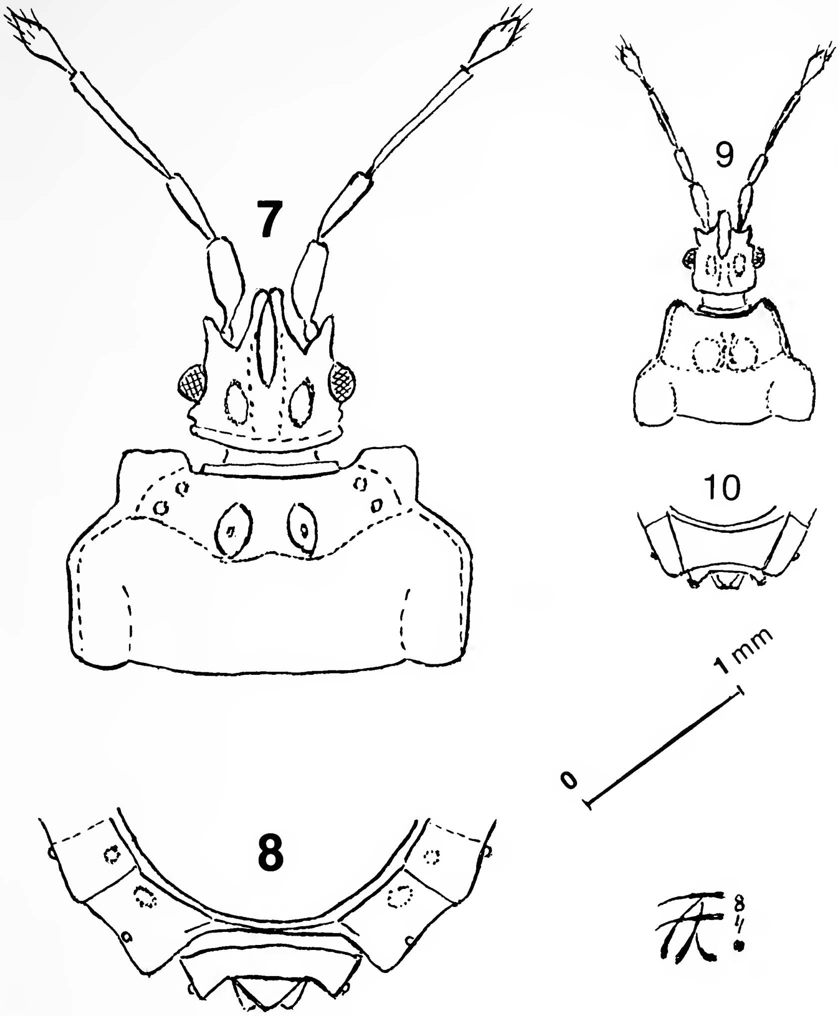
Glochocoris Usinger and Matsuda, 1959

Glochocoris borneensis, new species

Figs. 9, 10

Diagnosis. Glochocoris borneensis, new species, is related to *G. elongatus* Kormilev, 1960, but is larger, the antennae are relatively longer (2.55 times as long as width of head across eyes, 2.2 times in *G. elongatus*), and the abdomen is relatively narrower.

Description. Female. Elongate, slightly widening posteriorly; head and pronotum with dispersed granulation. HEAD: as long as width across eyes (11:11); anterior process tricuspidate anteriorly, reaching basal ⅖ of antennal segment I; antenniferous tubercles short, blunt, diverging; postocular borders rounded; vertex raised medially, with 2 (1 + 1) elongate callosities. Antennae 2.55 times as long as width of head across eyes (28:11); relative length of antennal segments I to IV 7:5:9:7. Labium reaching hind border of labial groove, which is closed posteriorly. PRONOTUM: shorter than maximum width (15:25); collar sinuate anteriorly; anterolateral angles rounded; lateral borders convex anteriorly and posteriorly, sinuate in middle, parallel at humeri; hind border sinuate. Fore disc with median sulcus, flanked by 2 (1 + 1) round callosities; hind disc transversely raised. SCUTELLUM: missing. HEMELYTRA: Corium with two veins forming a cell; membrane without veins. ABDO-



Figs. 7–10 7. *Notapictinus dollingi*, ♀. 7. Head and pronotum. 8. Apex of abdomen from above. *Glochocoris borneensis*, ♀. 9. Head and pronotum. 10. Apex of abdomen from above.

MEN: elongate-ovate, longer than maximum width (47:28); posteroexterior angles of connexiva not protruding; tergum VIII as wide as width of head across eyes (11: 11); paratergites of VIII truncate, reaching ⅔ of truncate segment IX. Spiracles II concealed; III and IV ventral; V to VII sublateral, slightly visible from above; VIII lateral, visible from above. COLOR: testaceous, eyes brown.

Measurements: Total length 3.52; width of pronotum 1.00; width of abdomen 1.12.

Holotype. ♀ N BORNEO, Samawang near Sandakan, Jungle, 12.VII.1927; ex F.

M. S. Museum, B M. 1955-354; deposited at the British Museum (Natural History) London.

Notapictinus Usinger and Matsuda, 1959

Notapictinus dollingi, new species

Figs. 7, 8

Diagnosis. Notapictinus dollingi runs in my key (1967:7–9) to *N. paramaculatus* Kormilev, 1960, but is larger, antennal segment IV is relatively shorter, and spiracles VI are lateral and VII dorsolateral.

Description. Female. Elongate-ovate; head and pronotum very finely punctured; connexivan bicolored brown and yellow. HEAD: slightly shorter than width across eyes (22:23); anterior process slighlty incised anteriorly, jugae longer than clypeus, reaching basal ⅖ of antennal segment I; antenniferous tubercle subacute parallel; postocular minute, not reaching outer border of eyes; vertex with 2 (1 + 1) ovate infraocular callosities. Antennae 2.3 times as long as width of head across eyes (53: 23); relative length of antennal segments I to IV 13:10:20:10. Labium extending to hind border of labial groove, which is closed posteriorly. PRONOTUM: shorter than maximum width (27:53); fore lobe narrower than hind lobe (40:53); collar truncate anteriorly; anterolateral angles expanded into large rectangular lobes, produced forward beyond collar, fore border sinuate laterad of collar, then truncate; lateral borders of fore lobe parallel; lateral notch forming obtuse angle; lateral borders of hind lobe parallel at humeri, converging anteriorly; hind border weakly convex. Fore disc with 2 (1 + 1) ovate callosities, 4 (2 + 2) small, round callosities laterad of them; hind disc with fine, dispersed granulation. SCUTELLUM: shorter than basal width (20: 30); lateral borders straight, carinate; median ridge robust, narowing posteriorly not reaching tip of disc; the latter roughly, transversely rugose. HEMELYTRA: almost reaching hind border of tergum VII; corium reaching ½ of connexivum III, outer border produced backward into long, narrow point; membrane with irregular veins, appearing wrinkled. ABDOMEN: ovate, longer than maximum width across segment IV (82:67); connexiva II and III fused; posteroexterior angles of connexiva protruding. Spiracles II to V ventral, far from margin; VI lateral, visible from above; VII dorsolateral; VIII lateral. Tergum VIII (♀) as wide as width of head across eyes (23:23). LEGS: femora finely serrate inferiorly. COLOR: head, antennae, pronotum (with exception of yellow anterolateral lobes), scutellum, clavus, corium, and legs red brown; connexiva red brown, yellow anteriorly.

Measurements: Total length 6.20; width of pronotum 2.12; width of abdomen 2.68.

Holotype. ♀ COSTA RICA, Turialba, Catie/iica Research Station; 24–30.VII.1981, W. R. Dolling, 1981-411; deposited in the British Museum (Natural History), London.

Etymology. It is a pleasure to dedicate this species to the collector, W. R. Dolling.

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A SYNOPSIS OF THE ZOOGEOGRAPHY OF THE RHYPAROCHROMINAE (HETEROPTERA: LYGAEIDAE)

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Abstract.—The distributions of the Rhyparochrominae are analyzed from the point of view of general patterns of occurrence, faunal composition of the major zoogeographic areas, and interpretation of the meaning of observed patterns.

This dedicatory issue honoring the hemipterological work of Dr. Richard Froeschner seems an ideal place and time to summarize what we know of one of the larger and more diverse taxa in the suborder Heteroptera. This paper is thus an attempt to place in perspective the present state of our knowledge of the distribution of the rhyparochromine Lygaeidae. It also offers some hypotheses to explain the zoogeographic patterns.

The Rhyparochrominae, the largest subfamily of Lygaeidae (Table 1), is particularly well suited for zoogeographic studies because the great majority of species are ground-living, litter-inhabitants. This geophily has enabled many species to develop flightless morphs when living in relatively stable habitats (Slater, 1976, 1978). This increases the probability that such species and genera will have restricted ranges and reduced dispersal ability. As piercing-sucking insects that feed on mature fallen seeds, they represent a group living at a very specialized trophic level.

Until recently distributional studies have been hampered by the lack of basic taxonomic knowledge at the specific level and because the relationships of the various tribes were poorly understood. The large amount of work accomplished during recent decades has brought the subfamily to the point where at least a preliminary survey is feasible. Such a survey is desirable because without an "overview" future workers will frequently overlook the significance of new information.

Despite the fact that many species (and a number of genera) remain to be described, the descriptions of new taxa in recent years has tended to reinforce existing patterns rather than change them. For the most part I do not think we are ready to attempt to distinguish vicariant from dispersal patterns although in places the reader will see what appears to be such interpretations. Generic endemicity is high (Table 2) but is probably in part due to regional, rather than world-wide taxonomic efforts.

One of the greatest needs is for a cladistic analysis of the genera of the various tribes. This has been accomplished only for the Myodochini (Harrington, 1980) and the Cleradini (Malipatil, 1983). In addition, if Slater and Woodward (1982) are correct, several tribes are not defined on the basis of synapomorphies and might therefore be unsuitable for biogeographic analysis.

The paper approaches the analysis in three ways: First, by segregating the tribes into general categories of distribution with a brief synopsis of each, second, by a

Table 1. Tribes of Rhyparochrominae. Number of genera and species.[1]

Tribe	Genera	Species
Antillocorini	26	101
Cleradini	19	48
Drymini	51	260
Gonianotini	21	113
Lethaeini	38	156
Lilliputocorini	1	8
Megalonotini	19	83
Myodochini	62	279
Ozophorini	25	116
Plinthisini	3(+)	111(+)
Rhyparochromini	38	352
Stygnocorini	13	56
Targaremini	23	60
Udeocorini	15	35

[1] The numbers in this and other tables do not conform precisely with the published literature. In some cases I have taken the liberty of listing genera in what I consider their proper tribe even though they have not been formally moved and have added species numbers for some still undescribed taxa.

discussion of the composition of major zoogeographic areas (Table 2); third, by an attempt to interpret the meaning of the various distributional patterns.

It is a pleasure to honor Dr. R. C. Froeschner for his contributions to Hemipterology and for his many years of assistance and encouragement to workers in the field. It is also to recognize, with affection, a long standing friendship going back to mutual graduate student days at Iowa State University.

GENERAL DISTRIBUTION PATTERNS OF THE TRIBES OF RHYPAROCHROMINAE

I. *Circumtropical*

Antillocorini. Greatest diversity and most plesiomorphic taxa in South America (Table 3). One large circumtropical genus (*Botocudo*) that also reaches oceanic Pacific Islands. Otherwise impoverished in Old World Tropics and Australia.

Lethaeini. Abundant and diverse in Africa, Asia and Australia. Phylogenetic ties between South America and Australia.

Ozophorini. Abundant and diverse in Neotropics; a secondary center of diversity in Oriental Region. Peripheral in Ethiopian region.

Lilliputocorini. A single genus of minute species found in Australia, New Guinea, Malaysia, Ceylon, Nepal, Ghana, and Brazil. (Štys, in litt., questions the monophyly of this tribe.)

II. *Old World Tropical*

Cleradini. Abundant and diverse in Oriental Region and northern portions of Australian Region. Close relationships among several Ethiopian and Oriental taxa.

III. *Old World Temperate*

Stygnocorini. Abundant and diverse in montane areas and southwestern Cape region of South Africa with related taxa in Tasmania, New Zealand, and the mountains of tropical Africa and Madagascar; secondary radiation in the Palearctic. Absent (except as introductions) in the Western Hemisphere. (Taxon possibly paraphyletic or even polyphyletic.)

IV. *Australian–South American*

Udeocorini. Distribution paralleling that of marsupials; a few strongly differentiated genera in South America; a large Australian fauna (Table 5) for the most part found in the Bassian subregion.

V. *Australian–New Zealand*

Targaremini. The most restricted distribution of any rhyparochromine tribe; a few genera in eastern Australia, but majority of taxa found on New Zealand, with several on New Caledonia and the New Hebrides.

VI. *Palearctic*

Gonianotini. Primarily Palearctic (Table 8), with extensive speciation in several genera; includes a generic level western Nearctic element.

Megalonotini. Distribution for the most part resembles that of Gonianotini with greatest diversity in the Palearctic (Table 8) and with a western Nearctic element differentiated at the generic level; a strongly differentiated genus present in South Africa associated with the southwestern Cape and Drakensberg Mountains, plus a few additional Ethiopian and Oriental genera. (The lack of a cladistic analysis and the difficulty of distinguishing members of the tribe from those of the Rhyparochromini without nymphs makes speculation of the origin useless at present.)

VII. *Primary Eastern Hemisphere*

Rhyparochromini. A large tribe abundant in the Palearctic, Ethiopian and Oriental Regions including northern Australia; absent from the Neotropics; a small, essentially Palearctic element in the Nearctic; a dominant and diverse group in the African savannah with many species and genera similar to the extensive Palearctic fauna. *Stizocephalus* distribution in SE Australia and New Zealand anomalous.

Drymini. Distribution parallels, in many respects, that of the Rhyparochromini; abundant and diverse in the Palearctic, Ethiopian, and Oriental Regions; absent from the Neotropical Region; relatively few Nearctic representatives, most of which are congeneric with those in the Palearctic (two endemic genera in the west); the major apparent difference between drymine and rhyparochromine distributions is the relatively greater diversity and degree of generic endemism of Australian Drymini.

Whereas the majority of species of Rhyparochromini are associated with savanna (often relatively temporary) habitats, the majority of drymine species appear to be associated with forest, forest edge, and mixed "bushveld" habitats. Some, such as

Table 2. Generic endemicity in the Rhyparochrominae.

Region	Number of genera	Number of endemic genera	% Genera endemic
Palearctic	73	48	66
Neotropical	65	40	62
Australian	74	38	51
Oriental	91	43	47
Ethiopian	88	40	45
Nearctic	50	17	34

the species of *Appolonius*, are arboreal. There is a diverse fauna feeding on seeds of *Ficus*. Many of the species are small and cryptic, others large and active flyers.

VIII. *World Wide Distribution*

Plinthisini. Taxonomy chaotic; until past 20 years almost all species placed in the genus *Plinthisus* and subgenera based only upon Palearctic species. The tribe was considered essentially Palearctic with the "usual" pattern of a few species in the western Nearctic. There is, however, an extremely rich and diverse (largely undescribed) South African fauna and many undescribed species from montane areas of tropical Africa. Slater and Sweet (1977) have described a rich Australian fauna with African relationships. The tribe is known to occur in South America (Slater 1971) and there is a diverse (largely undescribed) fauna in western North America.

Myodochini. Distribution most puzzling of any rhyparochromine tribe despite the fact that it is one of the few that has been the subject of a modern cladistic analysis. It is the dominant rhyparochromine element in the Neotropics with large numbers of genera and species (many as yet undescribed) and also very abundant individually. Harrington (1980) demonstrated that most of the plesiomorphic taxa also occur there. There is a large Nearctic element, mostly with Neotropical affinities. In contrast to the Nearctic the Palearctic fauna is impoverished and largely northern extensions of Ethiopian and Oriental taxa (with one Holarctic species of an essentially Nearctic genus, *Ligyrocoris sylvestris* F.). The fauna of the Old World tropics is extensive and contains some relatively plesiomorphic and morphologically isolated elements. The Australian fauna is essentially an extension of a few Oriental elements.

THE NEOTROPICAL REGION
Tables 3, 9

The neotropical fauna is the most disharmonic of any of the major faunal regions, consisting almost entirely of Myodochini, Ozophorini, Lethaeini, and Antillocorini. In fact, it is possible to collect rhyparochromine lygaeids in South America, tropical Central America, and the West Indies for weeks and never collect a specimen of any other tribe.

There are a few udeocorines and plinthisines but they constitute only 3% of the species and 4% of the genera. Tribes that are numerous and diverse in the Old World are absent. There are no representatives of the Rhyparochromini, Drymini, Mega-

Table 3. Neotropical distribution of Rhyparochrominae.

Tribe	% Total Neotropical genera	Number Neotropical genera	Number endemic genera	% Total Neotropical species	Number Neotropical species
Antillocorini	22	14	10	13	32
Cleradini	—	—	—	—	—
Drymini	—	—	—	—	—
Gonianotini	—	—	—	—	—
Lethaeini	17	11	7	13	30
Lilliputocorini		1	—	—	1
Megalonotini	—	—	—	—	—
Myodochini	40	26	15	49	117
Ozophorini	14	9	6	22	54
Plinthisini	2	1	—	1	2
Rhyparochromini	—	—	—	—	—
Stygnocorini	—	—	—	—	—
Targaremini	—	—	—	—	—
Udeocorini	5	3	2	2	5
		65	40		236

lonotini, Gonianotini, Cleradini, Stygnocorini or Targaremini. The absence of so many Old World tribes appears to have permitted the radiation and diversification of the Myodochini. At present 117 species distributed in 26 genera are recognized (49% of the species and 40% of all Neotropical genera) and many taxa are still undescribed.

If one collects in the Neotropics after collecting in Africa and Australia, it is at once evident that in shape, size, color, and habits myodochine taxa have come to occupy the ecological niches that are "filled" in the Old World by representatives of several other tribes (or other subfamilies). Sometimes convergence between members of different tribes is remarkable, as in the "pimple-like" eyes of *Bacacephalus* that closely resemble those of some species of *Salaciola* and *Ibexocoris* (both Drymini) in Africa. *Megacholula* closely resembles some species of African and Asian *Dinomachus* (Heterogastrinae). Species of *Cholula* and *Neocattarus* resemble the Paleotropical species of *Appolonius* (Drymini).

Some Ozophorini have also radiated, although less spectacularly than has the Myodochini. While there are some remarkably modified genera, such as the recently described *Icaracoris* Slater and *Allotrophora* Slater and Brailovsky, the radiation has been to a large extent within the genus *Ozophora*. Even if *Ozophora* proves to be paraphyletic, the ozophorines would still be less diverse in form than the myodochines. There are some striking cases of convergence (possibly Mullerian mimicry) between certain taxa of these two tribes. Fifty-four species of ozophorines distributed in nine genera (22% and 14% of the rhyparochromine fauna respectively) are recognized and there are many undescribed species.

The Lethaeini and Antillocorini are about equally diverse (Table 3). There are many undescribed taxa, but their proportion of the fauna is likely to remain much the same relative to the Myodochini and Ozophorini. The exception may be in the

Table 4. Nearctic distribution of Rhyparochrominae.

Tribe	% Total Nearctic genera	Number Nearctic genera	Number endemic genera	% Total Nearctic species	Number Nearctic species
Antillocorini	8	4	—	5	7
Cleradini	—	—	—	—	—
Drymini	12	6	2	21	32
Gonianotini	10	5	3	11	17
Lethaeini	8	4	—	6	9
Lilliputocorini	—	—	—	—	—
Megalonotini	2	1	—	1	2
Myodochini	46	23	11	40	60
Ozophorini	8	4	—	9	13
Plinthisini	2	1	—	3	5(++)
Rhyparochromini	4	2	1	4	6
Stygnocorini	—	—	—	—	—
Targaremini	—	—	—	—	—
Udeocorini	—	—	—	—	—
		50	17		151

numbers of species of Antillocorini. There are many undescribed species of the circumtropical genus *Botocudo* already in collections and, since these are minute insects, they may also be relatively poorly collected.

The known Neotropical fauna of Plinthisini consists of only two species. Unless these represent recent invaders from the Nearctic, there should be many more.

The Udeocorini also are poorly represented (Table 3) but these taxa are very interesting as none of the genera are at all closely related to one another. One is strongly convergent to species of *Clerada* (Cleradini) and appears to also feed on warm-blooded vertebrates. One can scarcely refrain from suggesting that the udeocorines are the lygaeid analogs of the marsupials, with their Australian radiation and possible South American elimination by the Myodochini.

A final comment on the disharmony of the Neotropical rhyparochromines and the radiation of the Myodochini and Ozophorini is to note that 42% of the myodochine species of the world (48% of the genera) occur there. For the ozophorines equivalent figures are 41% and 38% respectively.

NEARCTIC REGION

Tables 4, 9

The North American rhyparochromine fauna at first glance appears to be a simple one, consisting of genera and species derived from the Neotropics and also of taxa that appear to be of Palearctic origin. This would suggest that a "Nearctic" region as such does not exist. However, this is an oversimplification.

The problem is that our knowledge of the distribution of most myodochine taxa (the predominant Nearctic tribe with 46% of the genera and 40% of the species) is insufficient to determine how many of these represent tropical and subtropical North American taxa and how many are truly South American. That as many as 13 of the

Table 5. Australian distribution (including New Guinea) of Rhyparochrominae.

Tribe	% Total Australian genera	Number Australian genera	Number endemic genera	% Total Australian species	Number Australian species
Antillocorini	4	3	1	3	6
Cleradini	8	6	5	13	23
Drymini	18	13	6	12	21
Gonianotini	—	—	—	—	—
Lethaeini	15	11	7	13	23
Lilliputocorini	1	1	—	1	2
Megalonotini	—	—	—	—	—
Myodochini	19	14	5	15	26
Ozophorini	3	2	—	3	5
Plinthisini	3	2	—	9	15
Rhyparochromini	8	6	1?	15	27
Stygnocorini	1	1	1	1	1
Targaremini	7	5	3	5	8
Udeocorini	14	10	9	12	21
		74	38		178

23 Nearctic myodochine genera may be endemic argues for their origin in North America. This is not the case for the other "Neotropical" tribes however. There are no endemic genera of antillocorines nor lethaeines and only one (questionably valid) endemic ozophorine genus.

Given the above limitations, the Nearctic rhyparochromine lygaeid fauna closely parallels at the tribal level the situation in passerine birds (Mayr 1946), which have a predominant Neotropical component (70% of the genera and 60% of the species), and an equally distinctive, although smaller, Palearctic component (28–30% of the genera and 38–40% of the species).

The so-called "Palearctic element" in the Nearctic is very interesting for it includes conspecific taxa between Eurasia and North America, such as *Sphragisticus nebulosus* (Fallén) (Megalonotini), *Scolopostethus thomsoni* Reuter (Drymini), and *Trapezonotus arenarius* (L.) (Gonianotini), closely related, probably sister-species (in *Emblethis* (Gonianotini), *Eremocoris, Drymus,* and *Gastrodes* (Drymini), and *Peritrechus* (Rhyparochromini), and distinct endemic genera which occur almost without exception in western North America (Drymini: *Thylochromus* and *Togodolentus;* Gonianotini: *Atrazonotus, Claudinerobius, Delochilocoris, Malezonotus;* and Rhyparochromini: *Uhleriola.*) Unfortunately there has not been even a preliminary cladistic study of any of the tribes to which these genera belong so that we have no clear idea of their Palearctic relationships. The remaining taxa with Palearctic relatives are either confined to the western states or have the majority of their species there. There are no native stygnocorines in North American but *Stygnocoris rusticus* (Fallén) and *Stygnocoris sabulosus* (Schilling) have been introduced in the northeast. *Megalonotus sabulicola* Thomson (Megalonotini) has been introduced on both coasts. The other Holarctic species, however, belong to genera that have endemic North American species and their present distributions do not suggest recent introduction.

In summary, the Nearctic rhyparochromine fauna is an interdigitation of Neotropical and Palearctic elements with the former predominating. It is especially noteworthy for the diversity of taxa in the tribe Myodochini.

AUSTRALIAN REGION

Tables 5, 9

I have attempted, for the most part, to discuss major faunal regions as a whole and to avoid the complexities of intra-regional differences. However, to do so for the Australian Region would obscure the dichotomy of the rhyparochromine fauna (Slater, 1976). At the risk of some oversimplification, the Australian fauna can be segregated into two major components: old, chiefly autochthonous, and largely confined to the Bassian subregion, but with (chiefly) mesic elements in eastern and northeastern Queensland; and a relatively recent invasive element found primarily in the Torresian subregion.

The rhyparochromine fauna of the Bassian subregion (southwestern and southeastern Australia) is remarkable for the radiation and diversification of the Udeocorini. Many members of this tribe appear analogous both structurally and functionally to members of several other tribes in other parts of the world. One sees short, broad elliptical species resembling gonianotines, elongate, long-legged fast-running species that resemble Neotropical myodochines, etc. This radiation suggests antiquity and appears to be, as previously noted, a less spectacular but similar phenomenon to that exhibited by the Marsupalia.

A number of Plinthisini of the Bassian subregion show close relationships to those of the southwestern Cape area of Africa (Slater and Sweet, 1977). There is an endemic genus of stygnocorine (*Tasmanicola*) on Tasmania that is related to South African genera and there are distinctive lethaeine taxa. Thus, while udeocorines constitute only 14% of the Australian genera and 12% of the species, it is also true that 10 of the 15 known genera (67%) occur in Australia and that all 10 genera are endemic.

In contrast to the Bassian subregion, northern Australia has a large number of genera and species shared with the Oriental Region. This fauna is dominated by species of Rhyparochromini and Myodochini which live mainly in disturbed habitats.

The Targaremini are an old element of mesic habitats (see discussion of New Zealand fauna). The Lethaeini have affinities with South America on the one hand (O'Donnell, 1979) and with Africa on the other (Woodward and Slater, 1962). Superimposed upon these patterns is an Old World tropical component that mirrors the distribution of many myodochines and rhyparochromines.

The Australian drymine fauna is difficult to understand. There are a number of endemic genera, some of which are Bassian. Some taxa show close Oriental relationships. I have suggested (Slater, 1976) that the Drymini have spread and radiated in forest edge habitats at the expense of the older, more mesic-adapted Targaremini as Australia has become increasingly arid. However, one must say that until the large drymine fauna of Asia is better known it will be impossible to understand the true degree of endemism and the significance of this interesting fauna.

The fauna of New Guinea and its adjacent islands is much too poorly known to draw any meaningful conclusions. The rhyparochromine fauna of this area appears to have strong Oriental affinities, which is consistent with the faunal composition of

Table 6. Ethiopian distribution (excluding Madagascar) of Rhyparochrominae.

Tribe	% Total Ethiopian genera	Number Ethiopian genera	Number endemic genera	% Total Ethiopian species	Number Ethiopian species
Antillocorini	6	5	2	4	18
Cleradini	9	8	5	3	12
Drymini	15	13	8	14	57
Gonianotini	—	—	—	—	—
Lethaeini	15	13	5	11	44
Lilliputocorini	1	1	—	0.2	1
Megalonotini	9	8	4	5	19
Myodochini	14	12	4	10	39
Ozophorini	2	2	—	1	5
Plinthisini	1	1	—	10	40(+)
Rhyparochromini	21	18	9	35	142
Stygnocorini	8	7	3	7	27
Targaremini	—	—	—	—	—
Udeocorini	1?	1?	—	0.2	1?
		88	40		404

the Rhyparochrominae of Northern Australia (and also with that of other lygaeids such as the Blissinae). A species of *Udeocoris* (Udeocorini) reaches Timor but probably recently as it has not differentiated.

ETHIOPIAN REGION
Table 6

As we come to understand the Ethiopian fauna more adequately, it becomes apparent that at least three major faunas are present. One, essentially a savannah element, is dominated by species of Rhyparochromini and, to a lesser extent, Myodochini. A second, which is primarily a forest and forest edge fauna, is composed chiefly of species of Drymini and Lethaeini. The third, very distinctive fauna found chiefly in the southwestern Cape and in montane areas in both east and west Africa, contains many Stygnocorini and Plinthisini. There is also certainly a relationship between the faunas in the southern Cape Macchia and the Meditteranean Magreb but we do not know enough at present to evaluate this other than to say that it is not due to convergence. It is important to emphasize the abundance and diversity of the Rhyparochromini and Drymini in Africa since neither tribe has a single Neotropical representative.

Much of the tropical African fauna shows close relationship to the Oriental fauna (Table 9) and the two areas (except for the "old" component discussed above) really constitute more the "Paleotropical Kingdom" of botanical biogeography than separate zoogeographic "regions."

ORIENTAL REGION
Tables 7, 9

The lygaeid fauna of this large and important area has been relatively little studied in recent years. Earlier studies were extensive. It resembles that of Africa in being

Table 7. Oriental distribution of Rhyparochrominae.

Tribe	% Total Oriental genera	Number Oriental genera	Number endemic genera	% Total Oriental species	Number Oriental species
Antillocorini	6	5	—	7	23
Cleradini	6	6	4	3	11
Drymini	27	24	18	18	58
Gonianotini	—	—	—	—	—
Lethaeini	11	10	4	16	51
Lilliputocorini	1	1	—		4
Megalonotini	3	3	1	2	6
Myodochini	13	11	2	14	46
Ozophorini	11	10	7	9	30
Plinthisini	3	"3"	"2"	2	7
Rhyparochromini	18	17	5	28	91
Stygnocorini	—	—	—	—	—
Targaremini	—	—	—	—	—
Udeocorini	1?	1?	1?		1?
		91	43		327

rich in Rhyparochromini, Drymini, Lethaeini, and Myodochini. It differs in having a much more diverse ozophorine and cleradine fauna (Malipatil, 1983) in lacking Stygnocorini and (despite current recognition of three genera) apparently having a relatively limited plinthisine fauna.

PALEARCTIC REGION

Tables 8, 9

This great north temperate area is noteworthy for the extensive development of the tribes Gonianotini and Megalonotini, which constitute 42% of the genera and 33% of the species. In other regions these tribes are absent or constitute only a small part of the rhyparochromine fauna. Their abundance and diversity are the most striking features of the Palearctic rhyparochromine fauna.

Many Rhyparochromini and Drymini are present. A considerable number of genera have representation in either or both the Ethiopian or Oriental Regions.

There are no cleradines, udeocorines or targaremines, and few antillocorines, lethaeines, or ozophorines. In contrast, there appears to have been a modest secondary radiation of the Stygnocorini, and there is a large and varied plinthisine fauna.

It should be noted that most of the Rhyparochrominae of central and southern China and Japan are related to Oriental rather than Palearctic taxa.

NEW ZEALAND

The fauna of Rhyparochrominae is remarkable in consisting almost entirely of species of the tribe Targaremini (12 genera and 31 species are known). Of these 10 genera (83%) and all of the species are endemic. There is an endemic stygnocorine genus (*Margareta*), but the other species (a drymine, 2 rhyparochromines, a myodo-

Table 8. Palearctic distribution of Rhyparochrominae.

Tribe	% Total Palearctic genera	Number Palearctic genera	Number endemic genera	% Total Palearctic species	Number Palearctic species
Antillocorini	4	3	3	2	10
Cleradini	—	—	—	—	—
Drymini	15	11	6	20	90
Gonianotini	23	17	15	21	97
Lethaeini	3	2	—	2	8
Lilliputocorini	—	—	—	—	—
Megalonotini	19	14	9	12	55
Myodochini	10	7	4	4	20
Ozophorini	3	2	2	1	5
Plinthisini	1	1	—	12	55
Rhyparochromini	14	10	5	21	96
Stygnocorini	8	6	4	5	24
Targaremini	—	—	—	—	—
Udeocorini	—	—	—	—	—
		73	48		460

chine, a plinthisine and a lethaeine) are all species that also occur on the Australian mainland and possibly all are recent introductions. A fine paper by Malipatil (1977) treats the intra-island distribution of the New Zealand Targaremini in detail.

The antiquity and isolation of the targaremine fauna are evidenced by the percentage of species that are flightless and have developed coleopteroid front wings. According to Malipatil (1977) 95% of the species show wing modification. Malipatil (in litt.) has informed me that he believes the genus *Tomocoris* is not a targaremine. This genus is the only member of the tribe that occurs outside of the arc containing New Zealand, New Caledonia, Fiji, The Solomons, New Guinea, and Australia. If it is not a targaremine the percent of endemic genera and flightless species is well over 95%.

We do not have a cladistic analysis of the Targaremini and thus lack a hypothesis of where the more plesiomorphic taxa occur. Malipatil (1977) implies more than one colonization of New Zealand over water, but given the antiquity of New Zealand a vicariance scenario should not be ignored (and if demonstrated would be a major evidence for the minimum age of the subfamily).

MADAGASCAR

The (described) rhyparochromine fauna of this great island is so poorly known that very little can be said about it. Only 26 species representing 18 genera have been reported in the literature. I have examined 77 quite distinct species representing at least 40 genera, and this is probably only a fraction of the actual fauna. The only meaningful statement that can be made is that the affinities of the fauna are almost entirely African. Thirty-five species are definitely conspecific with African populations and there is no genus yet taken on Madagascar that occurs in the Orient that does not also occur in Africa. So many of the widespread African species occur on

Table 9. Rhyparochrominae: comparison of genera of faunal regions.

Regions compared	Total combined no. genera	No. genera only in two regions	No. genera endemic to two regions	% Genera endemic to two regions	No. genera in common	% Genera in common
Neotropical–Nearctic	91	17	74	81	24	26
Ethiopian–Oriental	145	8	91	63	34	23
Australian–Oriental	138	7	88	64	27	20
Australian–Ethiopian	162	2	80	49	22	14
Ethiopian–Palearctic	161	4	92	57	16	10
Palearctic–Nearctic	123	3	68	55	11	9
Palearctic–Oriental	164	1	92	56	13	8
Oriental–Nearctic	141	0	60	43	7	5
Nearctic–Ethiopian	138	0	57	41	6	4
Nearctic–Australian	124	0	55	44	5	4
Neotropical–Ethiopian	138	0	80	58	5	4
Neotropical–Australian	139	0	78	56	5	4
Palearctic–Australian	147	0	86	59	6	4
Neotropical–Oriental	156	0	83	53	5	3
Neotropical–Palearctic	138	0	88	64	2	1

Madagascar that one can only conclude that the Mozambique Channel is not an effective barrier for strong-flying, polyphagous seed-feeders such as species of *Pseudopachybrachius, Horridipamera, Dieuches, Diniella, Lachnestes, Elasmolomus,* etc. Only two genera in Madagascar do not occur in Africa and the taxonomic status of both is questionable. There appears to be a radiation of lethaeine species (and a genus of Ozophorini) whose closest African relatives are in the west African forest zone. There is also an important, although limited, South African–Madagascan element.

INTERPRETATION OF DISTRIBUTIONS

If one is to make an intelligent interpretation of rhyparochromine distribution it is necessary to try to understand the likelihood of the degree to which long distance dispersal and vicariance have played roles in determining where organisms are or are not. It might be supposed that long distance dispersal would be a major factor in rhyparochromine distribution, because many species fly readily as evidenced by their abundance at lights. They have also been reported at sea (Scudder 1968, Zheng and Slater, 1984), and high in the air (Glick, 1939). Most species feed upon mature fallen seeds, and while some species are restricted in host range others are essentially oligophagous. Thus, if these latter lygaeids are capable of reaching an area at a distance from an existing range, there would seem to be an excellent chance for successful colonization. Actually, this seems to be the case only to an extremely limited extent. There are a few species of rhyparochromines that must disperse readily across barriers. Examples are *Lachnestes singalensis* and species of *Pseudopachybrachius* (expecially of the *vincta* complex), *Paromius, Botocudo, Elasmolomus,* and *Remaudieriana.*

The distance between West Africa and South America at present is too great for most rhyparochromines to cross. The lack of any species of Rhyparochromini and Drymini in South America despite their abundance and diversity in Africa, strongly supports the idea that Rhyparochrominae do not by themselves at present reach South America from Africa.

The Hawaiian fauna is extremely depauperate. Only four genera (five species) occur. At least two of these have been almost certainly introduced recently by man and at least one of the others probably has been. New Zealand, as previously noted, has a very limited, disharmonious fauna. In contrast the Madagascaran fauna is very similar to that of Africa, with many species in common. The West Indian fauna also is disharmonious and lacks many genera that are present on the adjacent Neotropical and Nearctic mainlands. The fauna that is there for the most part is most closely related to the nearest mainland (Slater, in prep.)

The conclusion that seems warranted is that a great many rhyparochromines can cross "limited-distance" water gaps such as the Mozambique Channel but cross wider water gaps infrequently, and such crossing and subsequent colonization is limited to a relatively few taxa.

If long distance dispersal is not a major factor in explaining rhyparochromine distribution patterns it becomes especially important to attempt to establish a hypothesis for a reasonable minimal age for the group. Since they are seed feeders, radiation of the Rhyparochrominae has probably been coincident with the rise and diversification of the angiosperms. It does not, however, follow that lygaeids were not present earlier than angiosperms since even some modern species feed on the seeds of gymnosperms. Unfortunately, the fossil record of the Lygaeidae is very fragmentary and most known fossils are not earlier than the Oligocene. Oligocene and Miocene specimens are very similar to modern taxa. Bode (1953) has assigned some lower Jurassic fossils from Germany to the Lygaeidae and Ping (1928) has reported species from the Cretaceous of China. This does not mean that rhyparochromines are this old but it does suggest that an Upper Cretaceous–Early Tertiary diversification is a conservative working hypothesis.

Taxa that will be considered first are those with the most restricted distributions, such as the Targaremini and Udeocorini. The Targaremini, as previously noted, are chiefly a New Zealand and New Caledonian tribe and are absent from South America. This suggests that the targaremines originated sometime between 80 and 45 million years before present (m.y.b.p.). If they had differentiated earlier than 80 m.y.b.p., the Campbell Plateau, including New Zealand and New Caledonia, would have been in contact with West Antarctica (Raven and Axelrod, 1972; Rich, 1975), which in turn was in contact with South America. Unless extinction has taken place in South America, Targaremini should be there if they were on New Zealand and West Antarctica earlier than 80 m.y.b.p. A subsequent invasion of Australia is not difficult to understand as the Lord Howe Rise and Norfolk Ridge as well as the Campbell Plateau provided much easier access to flying insects between Australia and New Zealand than at present (although the barrier to mammals was complete). An alternative possibility is that the targaremines differentiated before New Zealand broke away from East Gondwanaland prior to 80 m.y.b.p. but did not reach South America because of barriers presented by the archipelagic nature of West Antarctica (Dalziel and Elliot, 1971). Only a cladistic analysis of the Targaremini can determine which of the above is the more likely hypothesis.

The history of the Udeocorini must have been quite different. Their distribution parallels that of the Marsupials. They appear to have originated either in the Neotropical or Nearctic region well after 90 million years before present m.y.b.p., or they should be present in Africa, but hardly later than 45 m.y.b.p. or they would have had difficulty crossing from South America through East Antarctica to Australia and *vice versa.* Their absence from New Zealand and New Caledonia also argues for their presence in Australia subsequent to the isolation of New Zealand. If the reasoning has validity, then the diversification of udeocorines in Australia must have been relatively late or they could have used the same route as the targaremines in reverse.

The above hypothesis is consistent with what is known of other taxa. There obviously was an abundant food source available for seed feeding lygaeids. Raven and Axelrod (1972: 1380) list a whole series of angiosperm and gymnosperm families present in the Cretaceous when Africa, South America, and Australia were connected with Antarctica, and New Zealand and New Caledonia are famous for their "archaic" seed-plant floras.

The distribution of the Stygnocorini is a more difficult problem because the tribe is absent from South America. This may be due to taxonomic problems: (1) our inability to distinguish stygnocorines from plesiomorphic antillocorines without immature stages (and we lack immature stages for nearly all South American taxa); (2) we may be dealing with a biogeographic artifact since the tribe is held together by a constellation of plesiomorphic characters and may be paraphyletic (Slater and Woodward, 1982).

Some taxa are undoubtedly "old." *Notiocola* Slater and Sweet is a cool-adapted genus that occurs in montane areas of South Africa and Madagascar and is closely related to a Tasmanian genus (*Tasmanicola*) and somewhat less closely to an endemic New Zealand genus (*Margareta*).

Raven and Axelrod (1972) believe that the separation of Africa from Antarctica apparently took place at least 90 m.y.b.p. which would be about 20 million years after austral Africa and South America separated. However, Rich (1975) says it was much earlier, in the late Jurassic or early Cretaceous (about 130 m.y.b.p.). (The tropical African–South American break is usually considered to be about 90 m.y.b.p.) Thus stygnocorines should have been present prior to 90 m.y.b.p.. If they actually are absent from South America and Raven and Axelrod's time scale is correct this may mean that they were not present prior to 120 m.y.b.p. when Australia, South America, and Africa were connected. Thus we may be gaining at least a glimmer of how old the "Y-suture" clade within the Rhyparochrominae really is.

There is no evidence that stygnocorines have ever adapted extensively to lowland tropical conditions. They probably speciated extensively in south temperate areas, and became decimated as Africa moved 15 degrees north, Australia became increasingly xeric and Antarctica became increasingly colder. In any event, Miocene uplift in eastern Africa provided a corridor northward, and Pleistocene climatic conditions would have favored diversification in Eurasia and on the African volcanic peaks. O'Rourke (1975) has shown that there is at least one distinct species of *Lasiosomus* (all closely related) on each east African mountain, and also on Mt. Cameroon. This closely parallels the situation in many passerine birds, which Moreau (1966) attributed to Pleistocene climatic deterioration and the lowering of vegetation belts so that contact was established (or dispersal distance greatly lessened) between populations now isolated on the mountains.

In contrast to the Udeocorini, Targaremini, and Stygnocorini, which have a temperate and basically an austral distribution, the Lethaeini, Antillocorini and Lilliputocorini are essentially pan-tropical. It is impossible to discuss vicariance relative to dispersal since we do not have any idea what the sister-group relationships are within the tribes. We can say with some degree of confidence that lethaeines are old. This is evidenced by the number of strongly-modified, frequently flightless genera of limited distribution in areas where relict stocks tend to "accumulate." Also, some genera in one hemisphere appear to be more closely related to genera in other hemispheres than to other genera in their own hemisphere (O'Donnell, in litt.) The Lethaeini appear to be a tropical and subtropical Gondwanaland group. They probably arose and diversified first in West Gondwanaland. Such a hypothesis would presume the presence of sister groups of relatively plesiomorphic types in South America and Africa with the Oriental and Australian faunas being successively derived from African and/or South American stocks. There is no way to determine this until intratribal relationships are better known.

The Australian Lethaeini fauna is certainly in large part composed of relatively recent "invading" elements from the north (Woodward, 1968; Slater, 1976). Certainly there has not been a radiation of Lethaeini in the the Bassian subregion of Australia, which one might have expected had they been on the continent a long time. All in all dispersal through the tropics seems probable. The Palearctic and Nearctic faunas are impoverished and consist of northern extensions of Ethiopian-Oriental or Neotropical taxa respectively.

The Antillocorini have their plesiomorphic taxa in the Neotropics (but see discussion of the Stygnocorini for difficulties of placement) where the tribe is most diverse. The "Holarctic" antillocorine fauna, like that of the Lethaeini, is depauperate and consists of northern "extensions" of tropical taxa. The Ethiopian fauna, while containing many undescribed species of *Botocudo,* is thus far surprisingly undiversified (reexamination of some rare montane genera described as Lethaeini is necessary), and the same can be said for the Oriental Region. Only *Botocudo* reaches Australia although there is an endemic genus in New Guinea. The tribe probably is an old pan-tropical group of at least West Gondwanaland origin and possibly earlier.

The distribution of the Ozophorini has been discussed by Slater (1972). In the Eastern Hemisphere, ozophorines are largely confined to islands and to areas of continents that are somewhat isolated or peripheral (Cape region of South Africa, mountains of Asia, southwest corner of Australia, rain forest of west Africa, etc.) They appear to be an old group with strong powers of dispersal but limited competitive ability. In the Neotropics they are abundant, widespread, and there is very active speciation in the genus *Ozophora.* Like the antillocorines and lethaeines the Ozophorini in the "Holarctic" are largely northern "extensions" of a tropical fauna. The Ozophorini are probably another tropical Gondwanaland group. They may, in fact, prove to be direct tropical or subtropical derivatives of the Stygnocorini (which some species resemble) and from which they are differentiated chiefly by loss characters.

The remaining tribes of Rhyparochrominae have very different distributions. Also, they are tribes that cladistically have a number of apomorphic features and can be thought of as the "advanced Rhyparochrominae."

Of these more advanced tribes the Gonianotini have the simplest distribution pattern. Most genera are Palearctic. The tribe conforms perfectly to the concept of a Holarctic group that arose in the Palearctic and crossed through Beringia into North America. Since the Bering Bridge was open in the midtertiary, it would seem reasonable to believe that this was the latest that the first representatives of the tribe could have reached North America and still have achieved the degree of differentiation that they have.

Most gonianotines are markedly dry-adapted and it is difficult to understand why they have not dispersed through Africa following climatic deterioration there unless they diversified in Eurasia after the radiation of the Rhyparochromini in Africa, with the later group presumably preempting the available habitats.

The distribution of the megalonotines is somewhat similar to that of the Gonianotini (they probably are sister groups), but there are important differences. The tribe is primarily Palearctic, and the Nearctic component consists only of a single Holarctic genus (plus a recent introduction). The most interesting feature of megalonotine distribution is the recent description (Slater and Sweet, 1973) of a flightless, morphologically isolated genus (*Dermatinoides,* five species) in the Southwest Cape and in the Drakensberg Mountains to the east. This distribution is parallel to that of some "ancient" stygnocorines (which occur with *Dermatinoides*), plinthisines, and, of course, many other insects and plants (Stuckenberg, 1969). There are two other endemic Ethiopian megalonotine genera and there is a species of *Proderus* in the Cape which is very similar if not identical to Palearctic forms. I cannot explain the existence of *Dermatinoides* in South Africa other than by believing that the Megalonotini have been in Africa for a very long time and that they are a relatively dry-adapted group that has had great habitat reduction during mesic periods and that has suffered in competition with dominant, pervasive rhyparochromine and myodochine species when savanna conditions again became widespread.

Whether the Megalonotini were once widespread over Africa and Eurasia, are a Palearctic group that reached Africa in the Tertiary, or an African group that has recently reached and diversified in the Palearctic cannot be determined until a cladistic analysis suggests what the plesiomorphic elements of the tribe are. Certainly the great morphological differences between long-legged, elongate-bodied, and presumably active species such as *Rollathemus,* broad, flattened, sluggish species like *Dermatinoides,* and elliptical, active species such as *Allocentrum* suggest a long period of time in subsaharan Africa.

The Cleradini is an Old World tropical group of relatively recent origin. Traditionally they have been thought of as being an Oriental and Australian group, but recent collecting has revealed a varied African fauna, and the Oriental and African affinities are close. Its absence (except by introduction) in the Western Hemisphere indicates that the Cleradini probably diversified no earlier than the Oligocene.

The Rhyparochromini, one of the largest tribes, is also one of the most difficult to understand. The absence of the tribe in the Neotropics and the "invading' nature of the Australian fauna (except as noted below) would seem to rule out conclusively the presence of this tribe as a Gondwanaland element. Thus, Rhyparochromini must not have been present (in numbers at least) in Africa 100 m.y.b.p. when Africa and South America were still connected in the tropics. Indeed, they must not have been there for a considerable time thereafter, for even through marine sediments show actual continental separation this could not have been much of a barrier for a long subsequent period to flying insects that can at present reach the Cape Verde Islands. Raven and Axelrod (1974) note that northeast Brazil and Gabon were separated by only a narrow strait 90 m.y.b.p.

There are few Rhyparochromini in North America and the ancestors of these could have reached there recently, probably through Beringia. This seems to limit the possibility that the tribe is a Laurasian element and leads to the conclusion that it is a relatively recently-evolved group.

The Rhyparochromini are by and large a relatively dry adapted group. In Africa they are the dominant savanna component both in taxa and individuals (see Slater and Wilcox 1973, for Senegal). Axelrod (1972) notes the spread of aridity over tropical Africa near the end of the Oligocene (30 m.y.b.p.) due to uplift and cold water flowing northward along the west coast (Benguela Current) initiated by Antarctic glaciation (Raven and Axelrod, 1974). This increasing aridity of Africa would favor a group like the Rhyparochromini, and would account for their abundance and dominance in Africa today. From Africa it is not difficult to visualize an expansion into the Oriental and Palearctic regions where the faunas still have close affinities (both at generic and even specific levels) with the present fauna of Africa. An African origin for the Rhyparochromini would help explain why the equally dry adapted Gonianotini have not succeeded in invading Africa and why the Megalonotini have the appearance of a relict (out-competed?) group.

Stizocephalus is the one genus that casts doubt upon the above hypothesis. This genus (Rhyparochromini) is confined to eastern Australia and New Zealand. It may be introduced on the latter as the same species occur in Australia, but it does not seem to be related to other Australian rhyparochromines such as *Dieuches* and *Elasmolomus,* which are widespread Old World tropical genera. If *Stizocephalus* does not have Oriental relationships then it suggests that the Rhyparochromini are older than hypothesized above.

Harrington (1980) concluded that the Myodochini probably originated in West Gondwanaland in the late Cretaceous. This may be true but the sister tribe, the Udeocorini does not appear to be established by a synapomorphy. Therefore, the possibility remains that paraphyletic taxa may be involved.

The distribution of *Ligyrocoris sylvestris* (L.) (Myodochini) suggests a movement from North America to Eurasia. This genus almost certainly originated in North America, where there are many common and widespread species and the sister taxa are there. *L. sylvestris* is the most boreal of any of the North American species. It also occurs in the northern Palearctic and probably reached Eurasia through Beringia not earlier than the late Pleistocene.

Plinthisines probably represent an ancient group certainly present before the break-up of Gondwanaland and probably before the separation of North America from Africa. They have no evident synapomorphy with the rest of the Rhyparochrominae.

In summary, the distinctly different distributional patterns exhibited by the various rhyparochromine tribes suggest great differences in time of origin, degree of dispersal, and early cosmopolitanism (or the lack of it). The subfamily thus offers an excellent opportunity for students interested in testing phylogenetic and biogeographic hypotheses upon a group where new information is still accumulating.

ACKNOWLEDGMENTS

I wish to extend my sincere thanks to Ms. Jane O'Donnell (University of Connecticut) for critically reading the manuscript, to many colleagues for stimulating discussions of biogeographic and systematic aspects of rhyparochromine distributions and relationships, and to Mrs. Elizabeth Slater (University of Connecticut) for extensive aid in the preparation of the manuscript.

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LIGYROCORIS BARBERI (HETEROPTERA: LYGAEIDAE), A NEW SEEDBUG FROM THE SOUTHEASTERN UNITED STATES WITH A DISCUSSION OF ITS ECOLOGY, LIFE CYCLE, AND REPRODUCTIVE ISOLATION

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Abstract.—*Ligyrocoris barberi* new species is described from southeastern United States. A key is presented to the nine species of *Ligyrocoris sensu stricto* in eastern United States. In Texas *L. barberi,* a pterygopolymorphic species, inhabits dry prairie communities where the bug feeds on ripe seeds of *Rudbeckia hirta* L. (Compositae). *L. barberi* is shown to be reproductively isolated by behavior from its nearest relative, the more northern *L. diffusus.*

Barber (1914) described *Ligyrocoris slossoni* from a male specimen collected by Mrs. A. T. Slosson at Lake Worth, Florida. In 1921 in his revision of the genus *Ligyrocoris,* Barber came to the conclusion that the unique holotype was imperfect, saying "the reddish coloration of the head and pronotum may be due to its immaturity." Accordingly, he omitted the species from his key to the species of *Ligyrocoris.* In 1924, based on a female specimen collected by W. S. Blatchley at Dunedin, Florida, he concluded that *L. slossoni* was a valid species, redescribed it, and placed it close to *L. sylvestris* (L.) For the next 30 years in his long and distinguished career he identified as *L. slossoni* specimens from throughout southeastern United States. Based on these determinations seen in many collections, I had assumed that the species whose ecology I had been studying in Texas was *L. slossoni.* However, when I had an opportunity to study the type-specimen of *L. slossoni* (USNM type 62528), in conjunction with two female specimens from Florida (Alachua Co., 6/24/1923 RLT; Gainesville, Fla. JRW 5413), I realized that two different species were being carried under the name *L. slossoni.* I also studied the above noted female specimen collected by Blatchley and confirmed that it is the true *L. slossoni.* From the sparse available evidence, *L. slossoni* itself appears to be a northern Florida endemic species which is apparently rare, as it is known only from these four specimens. The other species, which is being described here as new, is widespread through the southeastern states and is sympatric with *L. slossoni* in northern Florida. The reference to *L. slossoni* in Sweet (1963) actually refers to this new species.

I name this new species in honor of Harry G. Barber who contributed so much to our knowledge of North American Lygaeidae, including a revision of the genus *Ligyrocoris.* Further, I take pleasure in dedicating this paper to Dr. R. C. Froeschner, without whose kind assistance at the Smithsonian National Museum of Natural History I would not have resolved this systematic problem.

MATERIALS AND METHODS

The sources of the specimens of the type-series are indicated by the abbreviations given in the acknowledgments. The description and measurements of the holotype were made with the aid of a Wild M5 Stereomicroscope with a maximum magnification of 150×. All measurements are in mm. Illustrations were made with the aid of an ocular grid and graph paper. In the field and laboratory studies, the methods used are similar to those of Sweet (1964). Insects were collected by hand, using an aspirator. They were observed and reared in 20 mm deep plastic petri dishes containing natural ground litter, seeds, and methyl cellulose cotton. Water was provided in a vial stoppered with absorbent cotton. The insects were kept at room temperature under prevailing day lengths in the laboratory. Cool conditions for diapause studies were provided with refrigerator/incubator equipped with photoperiod controls.

Ligyrocoris barberi, new species

Figs. 1, 4, 5, 8, 10

Description. Hemelytron and thorax except for lateral bars on mesosternum pruinose, other body areas subshining; pruinosity heavier, bloomlike on anterior lobe of pronotum, anterior ½ of scutellum and anterior ½ of hemelytron. Head except apex of tylus, anterior lobe of prothorax, anterior ⅔ of scutellum and most of the venter dark brown; pronotal collar, posterior lobe of pronotum, apical ⅓ of scutellum, acetabula, metapleural flange, pale yellow-brown; tylus, coxae, distal ⅔ of femora and antennal segment 4 light reddish brown, legs and other antennal segments pale yellow; 3 obscure longitudinal infuscations on posterior lobe of pronotum (Fig. 5); hemelytron including epipleuron pale tan, conspicuously marked with ferruginous brown (Fig. 1), a post median transverse dark bar (fascia) extending from distal ⅓ of clavus completely to lateral margin of corium; small pale spot in medial angle of corium, larger pale spot posterior to fascia; membrane dark with bright white spot on apex, veins very obscurely paler.

Entire dorsum densely and evenly covered with erect hairs 0.25 long; shorter, suberect hairs on antennae, legs, and abdomen; silky adpressed hairs on pleura and thoracic sterna; head roughened or shagreened with micropunctures; anterior lobe of pronotum, pleura, and sterna faintly and sparsely punctate; posterior lobe of pronotum (Fig. 6), scutellum, and hemelytron (Fig. 1) with larger punctures; clavus with three rows of punctures, the medial 2 rows uneven, corium with row of punctures on each side of Cu, a row lateral to medial fracture, and a field of punctures in center of corium.

HEAD. Slightly exserted, relatively large, porrect, flattened in lateral view, with tylus relatively elongate (Fig. 4); head length 0.78, width 0.98, interocular distance 0.53, interocellar distance 0.34, preocular length 0.55, postocular distance 0.08; tylar sutures converging posteriorly, length of tylus 0.22, lorum (maxillary plate) distinctly swollen and polished, bucculae low, meeting in a V directly behind labium. PRONOTUM (Fig. 6). Transversely constricted into distinct lobes, the troughlike incisure breached by a slight median carina, anterior lobe globose and equal in height to

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Figs. 1–13. *Ligyrocoris* spp. 1–3. Hemelytra. 1. *L. barberi.* 2. *L. diffusus.* 3. *L. slossoni.* 4, 5. Head, lateral view. 4. *L. barberi.* 5. *L. diffusus.* 6–8. Pronotum, dorsal view. 6. *L. obscurus.* 7. *L. slossoni.* 8. *L. barberi.* 9, 10. Abdomen, lateral view. 9. *L. barberi.* 10. *L. obscurus.* Figs. 11–13. Fore femur, sublateral view. 11. *L. barberi.* 12. *L. delitus.* 13. *L. slossoni.* s, stridulitrum. Scales lines equal 0.1 mm.

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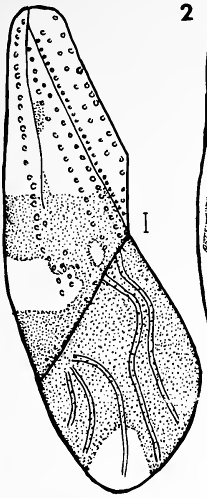

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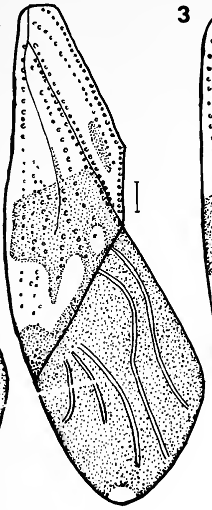

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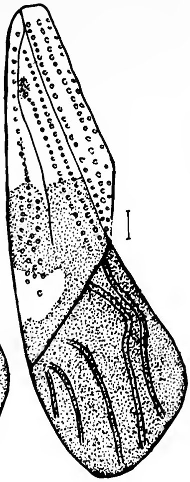

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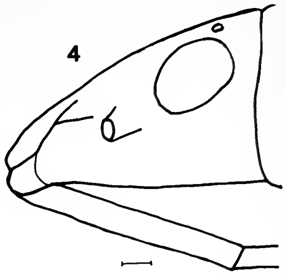

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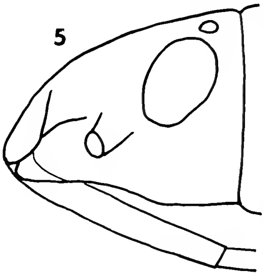

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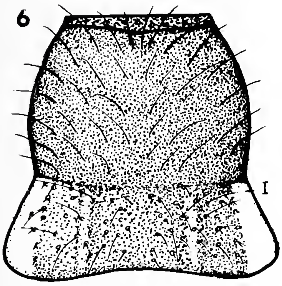

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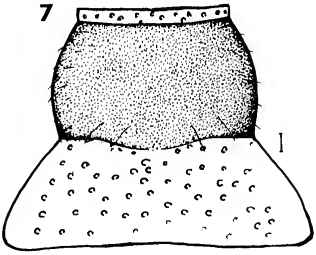

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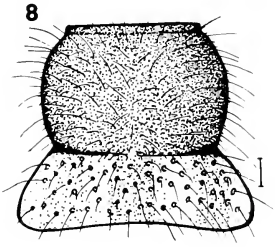

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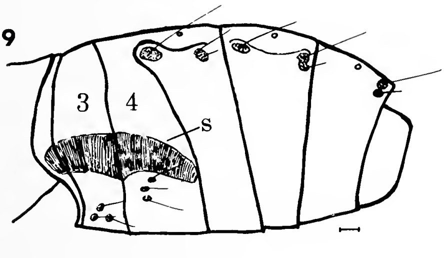

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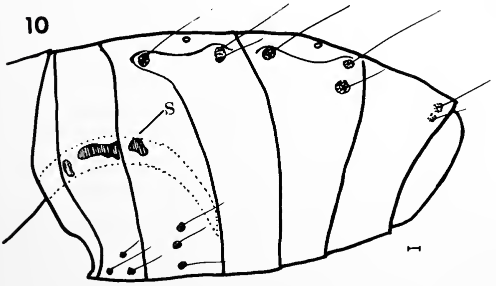

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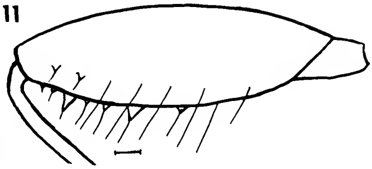

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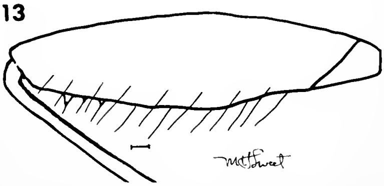

MHSweet

posterior lobe; the narrow anterior collar an impressed ring, not set off by a distinct incised line; length of pronotum 0.97, anterior lobe 0.63; width of anterior lobe 0.93, posterior lobe 1.20. SCUTELLUM. Little longer than wide (0.80:0.70) with low median carina. HEMELYTRA. Brachypterous (submacropterous), extending to ½ length of tergum 7; lateral margin of corium nearly straight, length of corium 1.80, width 0.60, length of commissure 0.40, distance from apex of clavus to apex of corium 0.70; distance from apex of corium to apex of membrane 0.49. *Mesopleuron* neither swollen nor visible from above; mesepimeron barely closed, metepisternum contacting mesepisternum; evapatorium small, restricted to lower ¼ of metapleuron and mesepimeron and extending dorsad along meso-metapleural segmental suture, auricle not calloused. ANTENNAE. Segments 1–3 terete, 4 fusiform, thickest (0.11); length of segments I 0.35, II 0.96, III 0.95, IV 1.05. LABIUM. Elongate, attaining fourth (third visible) abdominal sternum; labial lengths I 0.75, II 0.85, III 0.86, IV 0.40. LEGS. *Fore femur* (Fig. 11) moderately incrassate, width 0.38, length 1.27, armed on inner distal ventral surface with two large and 5–6 smaller spurs, each bearing a slender long seta; two small distal spines and row of long setae on outer under surface of femur; *mesotibia* with 4 rows, protibia and metatibia with two rows of moveable pale spines; length of metatibia 1.60, lengths of metatarsomeres I 0.66, II 0.18, III 0.15; plectrum a field of 19–20 tubercles on inner proximal surface of metafemur; stridulitrum (Fig. 11, s) a broad striate arc extending from sternum II to sternum IV, striae 0.046 apart. Total length 4.5.

Holotype. Brachypterous ♂, TEXAS. *Brazos Co.,* College Station, July 25, 1964, M. H. Sweet, deposited in National Museum of Natural History, Washington, D.C.

Paratypes. 6♂♂, ♀, same data as holotype, also deposited in J. A. Slater and British Museum collections. ALABAMA. ♀, Alexander City, Aug., G. Nelson (LSU). ARKANSAS. ♂, De Queen, VI-6-1951, L. D. Beamer (SMK). FLORIDA. *Duval Co.,* 2♂, ♀, (NMNH). GEORGIA. ♀, Stone Mountain, VIII-3-13. ILLINOIS. ♂, Dubois, Aug. 10, 1917 (UIU). KANSAS. *Boubon Co.,* ♀, Redfield, 1 mi N, July 13, 1966, Jean & Wilton Ivie (SMK). MISSISSIPPI. 2♀, Fulton, 7-14-30, R. H. Beamer; ♂, ♀, Wiggins, August 15, 1936, H. M. Harris (NMNH). MISSOURI. *Adair Co.,* ♀, Thousand Hills State Park, VII-3-1975, S. E. Thewke (SMK). NORTH CAROLINA. ♂, 2♀, Valley of Black Mts., July 9, 1906, W. Beuttenmuller; 2♀, ♂, *ibid.,* August 9, 1906 (NMNH). OKLAHOMA. ♀, Idzbel, 10-VI-31, C. C. Deonier. TEXAS: *Brazos Co.,* 3♂♂, ♀, College Station, Sept. 14, 1964; ♀, *ibid.,* Sept. 14, 1964; ♀, *ibid.,* Sept. 20, 1964; 13♂, 8♀, *ibid.,* April 23, 1965; ♂, 3♀, *ibid.,* July 8, 1965; ♀, *ibid.,* Oct. 10, 1965, 6♂, 10♀, *ibid.,* Oct. 15, 1979, ♂, 4♀, *ibid.,* Oct. 22, 1965; 2♀, *ibid.,* Oct. 10, 1976; 11♂, 21♀, *ibid.,* Oct. 15, 1979; ♂, 4♀, *ibid,* Nov. 8, 1979 (MHS, JAS, BM); ♂, Navasota, Texas, 5-12-1948, M. Polhemus. ♀, *Burleson Co.,* 3 mi E of Lyons on FR 60, 8-VI-1974, H. Greenbaum, sweeping (TAMU).

Diagnosis. Because it has a complete transverse dark fascia (Fig. 1) on the corium like *L. slossoni* (Fig. 3), *L. barberi* was confused with this species. *L. slossoni* has a unicolorous dark red head, reddish femora and tibia contrasting with yellow tarsi. The pronotum (Fig. 8) is nearly nude except for a few hairs, and there is only one major fore femoral spine (Fig. 12). *L. barberi* has instead a dark brown head and the unicolorous pale yellow tibia and tarsus. The pronotum (Fig. 8) is densely hairy, and there are two major fore femoral spines (Fig. 11). *L. slossoni* is actually more closely related to *L. litigiosus* in having a distinct groove demarcating a punctate pronotal collar (Fig. 8), and in having a shiny metapleuron. In *L. barberi* and most other species of *Ligyrocoris sensu stricto,* the metapleuron is pruinose and the pronotal collar is not set off by a distinct groove (Fig. 6).

In my key (Sweet, 1963) to the northeastern *Ligyrocoris, L. barberi* will run to *L. diffusus.* From *L. diffusus, L. barberi* can be told by its complete post-median, transverse fascia (Fig. 1) which broadly attains the lateral margin of the corium, its large, pale apex of the membrane, its more elongate and porrect head (Figs. 4 and 5) and its very long labium which reaches abdominal segment 4. In *L. diffusus* the fascia (Fig. 2) does not quite attain the lateral corial margin, the membrane has a small white apex, and the labium reaches only the metacoxae. *L. barberi* is a smaller, more brightly colored species of which most specimens are submacropterous, whereas *L. diffusus* is usually macropterous, especially in the zone of sympatry between the two species.

KEY TO SPECIES OF *Ligyrocoris* SENSU STRICTO OF THE UNITED STATES EAST OF THE 100th PARALLEL[1]

1\. Stridulitrum (Fig. 10, s) inconspicuous, only striate spots clearly visible on lateral side of abdominal sterna 3 and 4, the stridulitrum otherwise obscured by fine hairs; pronotum (Fig. 6) weakly constricted dorsally into lobes .... *obscurus* Barber

– Stridulitrum (Fig. 9) extending sublaterally as a broad conspicuous striate arc devoid of hairs from sternum 2 to sternum 4; pronotum (Figs. 7, 8) strongly constricted both laterally and dorsally into lobes 2

2\. Metapleuron subshiny like abdomen; pronotal collar set off by a sharply incised linelike groove (Fig. 7) 3

– Metapleuron pruinose like rest of thorax; pronotal collar an impressed ringlike area, not set off by a distinct groove (Fig. 8) 4

3\. Corium (Fig. 3) with a post-median, dark, transverse fascia; membrane unicolorous dark; head and femora distinctly unicolorously reddish, not mottled .....*slossoni* Barber

– Corium with lateral margin pale, membrane mottled dark and pale, head dark brown, femora pale mottled with dark spots .... *litigiosus* Stål

4\. Femora armed beneath distally with one or two small spines (Fig. 12); anterior lobe of pronotum pale or mottled .... *delitus* Distant

– Femora armed beneath with two large spines and 5–6 smaller spines (Fig. 11); anterior lobe of pronotum unicolorous dark brown 5

5\. Entire dorsum densely covered with long, erect hairs (Fig. 8), labium extending to metacoxae or abdomen; femora (Fig. 11) with many setae, these longer than width of tibia 6

– Dorsum with a few scattered, erect hairs (as Fig. 7), labium short, extending only to mesocoxae, femora with few setae, these shorter than width of tibia 7

6\. Fascia not extending completely to lateral margin of corium (Fig. 2), labium extending to metacoxae .... *diffusus* Uhler

– Fascia completely attaining lateral margin of corium (Fig. 1), labium long, attaining abdominal sternum 4 .... *barberi,* new species

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[1] Excluded from the key are species moved by Harrington (1980) to *Froeschneria: L. piligerus* Stål (=*L. abdominalis* Guerin-Meneville) and *L. multispinus* Stål (=*L. confraternus* Barber). The western USA and Mexican species of *Ligyrocoris* are being studied and will be treated in a later publication. The western "*L. diffusus*" and "*L. delitus*" populations each evidently comprise complexes of closely related species.

7. Basal metatarsomere twice combined length of distal tarsomeres (67:33); size small, length 4.77 to 5.18; metapleura never inflated and visible from above ..... *carices* Sweet
– Basal metatarsomere nearly three times combined length of distal tarsomeres (92:34); size larger (5.16 to 7.47) 8
8. Post-median, transverse fascia fuscous and broadly attaining lateral margin of corium; labial segment III longer than I (0.70:0.63); pale spot at mesal angle of corium faint or absent; basal and apical spots on membrane never confluent: fore femora usually fuscous .... *sylvestris* (Linnaeus)
– Post-median transverse fascia weak, ferrugineous, often absent; labial segment III shorter than I (0.57:0.67); basal and apical pale spots on membrane usually confluent, fore femora usually light yellow brown .... *depictus* Barber

Variation. L. barberi is pterygopolymorphic throughout its range. In the macropterous form, the wings fully exceed the posterior end of the abdomen (tergum 7). In the brachypterous form, which is much more common (88% of specimens of type-series), the wings attain but do not exceed tergum 7. In coloration some probably more teneral specimens are lighter pigmented and have somewhat reddish abdomens, femora, antennal segments, and heads. The obscure infuscations on the posterior lobe of pronotum are frequently absent.

Two specimens, one from Chicago, Illinois, and one from Hamar, North Dakota (7-27-37, C. L. Johnson), resemble *L. barberi* in size, investiture, and coloration, but are excluded from the type-series because the labium does not attain the abdomen, and the head is much more convex in front of eyes, much as in *L. diffusus* (compare Figs. 4 and 5). These specimens are like *L. barberi* but different from *L. diffusus* in being smaller and having the dark, transverse fascia extending completely to the lateral margin of the hemelytron. These specimens may represent yet another species of the *Ligyrocoris* complex, one well to the north of the known range of *L. barberi,* but more specimens and experimental studies are needed to test this hypothesis.

Distribution. L. barberi, as indicated by the above records, ranges across southeastern USA and is sympatric with *L. slossoni* and *L. litigiosus* in Florida, and overlaps the range of the closely related *L. diffusus* in Arkansas, Illinois, Kansas, North Carolina, and Oklahoma. *L. barberi* is probably the species identified from Missouri by Froeschner (1944) as *L. sylvestris,* which otherwise has a boreal range (Sweet, 1964).

Ecology. While a widespread species, *L. barberi* is relatively uncommon overall and is infrequently encountered in general collecting. In Texas, despite my extensive collecting throughout the state, I have encountered the species only in College Station, which probably merely reflects the intensity of local collecting around College Station in my biological studies on the Lygaeidae. I was able to study two populations for several years in different locations in the College Station area.

At both locations *L. barberi* was found on the ground in open areas in dry prairie habitats where *Rudbeckia hirta* (L.) (Black-eyed-Susan), its annual composite host plant, grew with other forbs among scattered grass clumps, chiefly *Schizachyrium scoparium* (Michx.) Nash admixed with some *Aristida* sp. and *Paspalum* spp. In one location the surface soil was sandy, in the other, clayey. In constrast to *L. diffusus,* which was abundant in early successional as well as old field communities, *L. barberi* was not found in early successional communities in Texas, despite the large invasion of *Rudbeckia* into such communities. As is usual in rhyparochromine lygaeids (Sweet, 1964), the predominantly brachypterous condition of *L. barberi* correlates with the relatively permanent habitats of the insect. However, it is difficult to evoke this as the reason for the insect's apparent absence in early successional stages and roadsides since its host plant, *Rudbeckia,* a natural component of the southwestern prairie community, is abundant in such successional habitats and forms stands which are in essential continuity between prairies and roadsides. Competition with other seed-feeding rhyparochromines may be involved, especially with relation to the life cycle of *L. barberi.*

Life history. The life cycle of *L. barberi* revolves around that of its host, which begins blooming in late spring and largely finishes seed production in midsummer (July) in College Station. When starving in the laboratory, *L. barberi* fed on other composite seeds such as *Helianthus annuus* L. (sunflower), but the insect did not complete its life cycle from egg to egg (first generation) except on ripe *Rudbeckia* seeds. Survival of adults was poor on all other seeds, including sunflower seeds. As in *L. diffusus* (Sweet, 1964), the insects carry *Rudbeckia* seeds about and aggressively defend them from conspecifics, especially of the same sex.

The phenology described here is based on data from the two populations of *L. barberi* in College Station, Texas. Like the more northern *L. diffusus* (Sweet, 1964), there were only two generations a year of the insect in Texas despite the long, warm season. Like most other members of the *L. diffusus* complex (Sweet, 1964), *L. barberi* overwintered as eggs in diapause. The eggs hatched in March and the nymphs fed on overwintered, fallen, ripe seeds of *Rudbeckia.* This generation became adult from late April to June. In May late-instar nymphs and adults often ascended the plant to feed on the ripening seed heads of *Rudbeckia.* The spring generation began laying its eggs at this time, and the young nymphs of the second generation developed on the *Rudbeckia* seeds now falling to the ground. By early July the second generation adults appeared. The presence in early July of first to fifth instar nymphs at the same time as the second generation adults attests to the extended oviposition period by the first (spring) generation adults. In the laboratory, the spring generation females laid eggs over a period of several months at a rate of 5–6 a day. The second generation adults were immediately sexually active in July, unlike *L. diffusus* which first entered a brief reproductive diapause that lasted until late August or early September (Sweet, 1964). However, *L. barberi* females did not oviposit until October. Since it is relatively warm through October in Texas, this probably indicates a photoperiodic control of oviposition and production of diapause eggs similar to *L. diffusus* (Sweet, 1964). From October to December females laid eggs that entered diapause in the anatrepsis embryonic stage much as does *L. diffusus* (Sweet, 1964). Diapause eggs laid in the laboratory and placed in petri dishes in the original field environment hatched in early March at the same time as the field population. Kept in warm conditions (ca. 24°C) in the laboratory the eggs died in diapause. Kept in cool conditions (5°C, 10 hour photoperiod) in an incubator, some eggs hatched in March when restored to normal conditions, but most eggs died.

From an adult female a parasitic tachinid fly *Catharosia* sp. emerged and pupated on Nov. 8, 1979. Since *Ligyrocoris barberi* overwinters as eggs, the fly must either change hosts to overwinter or wait as a pupa or adult until new *Ligyrocoris* nymphs are available in the spring for parasitism. *Catharosia* spp. parasitize several rhyparochromine lygaeid species, including *Ligyrocoris* spp. (Sweet, 1964).

The overall scarcity of *L. barberi* compared to *L. diffusus,* its northern counterpart, may be better understood in relation to its life cycle. It is the only lygaeid in east central Texas known to overwinter as diapause eggs. The other species in the area overwinter only as adults, except for a few which evidently have no diapause and survive the winter in most stages. The second generation adults of *L. barberi* must survive from July to October when oviposition begins, and the diapause eggs must escape predation and dehydration through the mild winter to hatch in spring. In this mild climate adults, perhaps because of their mobility, evidently have an advantage for overwintering in diapause. In this context it is significant that at each location where *L. barberi* was found, the insects disappeared with concomitant massive invasions of fire ants (*Solenopsis invicta*). It seems possible that increased predation pressure exerted by fire ants may have disrupted the already delicate population dynamics of *L. barberi* in the area. I have not found *L. barberi* in the College Station area for the past 6 years despite careful searching for this species.

Reproductive isolation. Since the populations of *L. barberi* at College Station, Texas occurred in similar habitats, fed on similar seeds (*Rudbeckia hirta* L. = *R. serotina* Nutt, in Sweet, 1964), and have a similar phenology as the more northern *L. diffusus,* the question was originally raised as to whether these southern populations represented a distinct species ("*L. slossoni*") or constituted instead a distinctive southern subspecies of *L. diffusus.* Accordingly, similar to the studies made on reproduction isolation on species of *Ligyrocoris* in northeastern U.S.A. (Sweet, 1963, 1964), mating trials were run between *L. diffusus* and *L. barberi.* First (spring) and second generation (summer) females were used in both species. In different years three sets of trials were run, one set with *L. diffusus* from Colorado, the second set with *L. diffusus* from Wisconsin, and the third set with *L. diffusus* from Connecticut. Virgin females were reared in the laboratory from each population and potential reciprocal crosses were arranged between individual males and females. In control crosses between males and females of the same species all viable individuals mated and fertile eggs were copiously laid (5–6 eggs per day, > 100 eggs per female). The experimental crosses consisted of two types. In the first experimental series a male and a female were left together continuously, and any resulting oviposition and fertility were recorded. At least ten viable replicates of each trial set were run. In the second experimental series, mating trials were run and the sexual responses of the individuals monitored. At least ten observations of mating reactions of each trial set were run. Some individuals used in the first experimental series were sometimes used in the second experimental series.

In all experimental crosses between *L. barberi* and *L. diffusus* the females of each species behaved as though they were virgin females (Sweet, 1964) and laid only a few (3–10) infertile eggs. In behavioral trials, the males of each species reacted vigorously to the presence of females by initiating a courtship dance in which the male stridulates as he dances, much as observed by Sweet (1963, 1964) and Thorpe and Harrington (1981). The receptivity of a female was determined by exposing her to a male of her own population but not permitting copulation. Only receptive, unmated females were used in cross-population reciprocal trials. In each case, a receptive female vigorously evaded the male of the other species population. The males did not appear to discriminate between females of the two species and courted each equally. These experimental data, in conjunction with the morphological discontinuity and with distributional evidence for a broad zone of sympatry, support the specific status of *L. barberi.*

Working with Wisconsin populations of *L. diffusus,* Thorpe and Harrington (1981) demonstrated, as hypothesized by Sweet (1963, 1964), that on contact with receptive females the males stridulate during the mating dance. However, Thorpe and Harrington discovered that male stridulation was not necessary for copulation to occur.

Although it was unobserved in my earlier studies (Sweet, 1963, 1964), I noted that a receptive female of *Ligyrocoris* spp. also often stridulated briefly when first approached by a male of her species. This movement, one or two strokes, was very quick and therefore readily missed while observing the vigorous activity of the males. This is significant since the female possesses the same stridulatory mechanism as the male. Nonreceptive females and females of the other species did not display this behavior and instead engaged in active avoidance behavior as described by Sweet (1964). It is difficult to accept this complex stridulatory behavior elicited so readily in courtship as being merely to function "in a pair maintenance capacity," as hypothesized by Thorpe and Harrington (1981), because other related species (tribe Myodochini) that do not stridulate copulated as readily in the laboratory as *Ligyrocoris* spp. In the laboratory after copulation, in both stridulating and nonstridulating species, the pairs showed no special "pair maintenance" and in each, males and females similarly went their separate ways. I will continue to investigate the role of stridulation in more detail in more naturalistic settings. Given that the stridulatory apparatus has been accepted as a major generic character in the Myodochini by Barber (1921) and Harrington (1980), it needs emphasizing here that *Zeridoneus costalis* (Sweet, 1964), *Z. knulli* Barber, and an undescribed species of *Zeridoneus* (Sweet, unpublished), which appear to lack the stridulatory apparatus, display a similar courtship dance to that of *Ligyrocoris* in which stridulating-like movements are made. As noted earlier (Sweet, 1964), in *Zeridoneus* the epidermal cells are aligned in parallel rows essentially as seen in the distinctive stridulitrum of *Ligyrocoris s.s.* (Fig. 9). This merits careful study, as the condition in *Zeridoneus* may be the primitive precursor leading to the evolution of the well-developed stridulatory structures in *Ligyrocoris. Ligyrocoris obscurus,* which has a definite but inconspicuous stridulitrum (Fig. 10), otherwise closely resembles species of *Zeridoneus* in its pronotal structure (Fig. 7), size, and coloration and may prove to be cladistically congeneric with *Zeridoneus.*

ACKNOWLEDGMENTS

I wish to thank the Texas A&M Fund for Organized Research for financial assistance in 1964. I give thanks for the loan of specimens from the following institutions and individuals: the National Museum of Natural History (NMNH) by R. C. Froeschner; J. A. Slater's personal collection, (JAS); Snow Entomological Museum, University of Kansas (SMK) by P. D. Ashlock; P. D. Ashlock's personal collection (PDA); Texas A&M Insect Collection (TAMU) by J. C. Schaffner; Florida State Collection of Arthropods, Gainesville (FSC) by Frank W. Mead; University of Illinois, Urbana (UIU) by J. K. Bouseman; Enns Entomology Museum, University of Missouri–Columbia (EMM) by T. R. Yonke; Louisiana State University Insect Collection (LSU), by J. B. Chapin; and Canadian National Collection Ottawa (CNC), by K. G. Hamilton. Specimens loaned from other museums not acknowledged here will be cited in a later publication on the western North American *Ligyrocoris.*

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J. New York Entomol. Soc. 94(2):291–295, 1986

FROESCHNEROCORIS DENTICAPSULUS, A NEW GENUS AND NEW SPECIES OF PYRRHOCORIDAE (HETEROPTERA: PYRRHOCOROIDEA) FROM THE ORIENTAL REGION

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Abstract.—The new pyrrhocorid genus *Froeschnerocoris* and new species *F. denticapulus,* are described from Assam in northeastern India. Its relationship to the genus *Dysdercus* is discussed, with special significance given to the structural differences in the metathoracic scent-gland ostiole and male and female genitalia.

During a revision of the genus *Dysdercus* Guerin-Meneville of the Indo-Pakistan Subcontinent, we had the opportunity to study a series of specimens from Assam in northeastern India lent by Dr. R. C. Froeschner at the National Museum of Natural History, Washington D.C. (USNM). On first inspection, the specimens appeared to resemble a small *Dysdercus* with predominantly red hemelytra and the apex of corium acute, but a closer examination showed that they represented a new genus. They differed from all known species of *Dysdercus* (Freeman, 1947) in having a markedly convex outer corial margin, which gives the body a more or less elongate-oval appearance; the longer, basal antennal segment about 1.5 times longer than head; and the bizarre genitalia with marked serrations or denticles on the ventroposterior portion (tongue) of the pygophore, spinous-type curved-blade parameres, and unique aedeagus and female genitalia.

Based on these specimens we describe *Froeschnerocoris* in honor of Dr. R. C. Froeschner, to acknowledge his long painststaking service and valuable contributions to the systematics of Hemiptera. All measurements are in millimeters.

Froeschnerocoris, new genus

Diagnosis. Most closely related to *Dysdercus* in the acute apex of corium, general body shape, and lobelike peritreme of the metathoracic scent gland ostiole, but easily separated by the small body size, parameres with large spinelike tooth, and other characters as noted in the description.

Description. Body relatively small. Head longer than broad; eyes sessile; basal antennal segment about 1.5 times length of head, 3rd segment shortest, basal segment longest and slightly longer than 4th; labium extending beyond hind coxae to 3rd abdominal venter, 2nd labial segment longer than 3rd, 4th shortest. Pronotum with lateral margins reflexed; ostiolar peritreme large, lobe-like; membrane of hemelytra extending beyond apex of abdomen in both sexes.

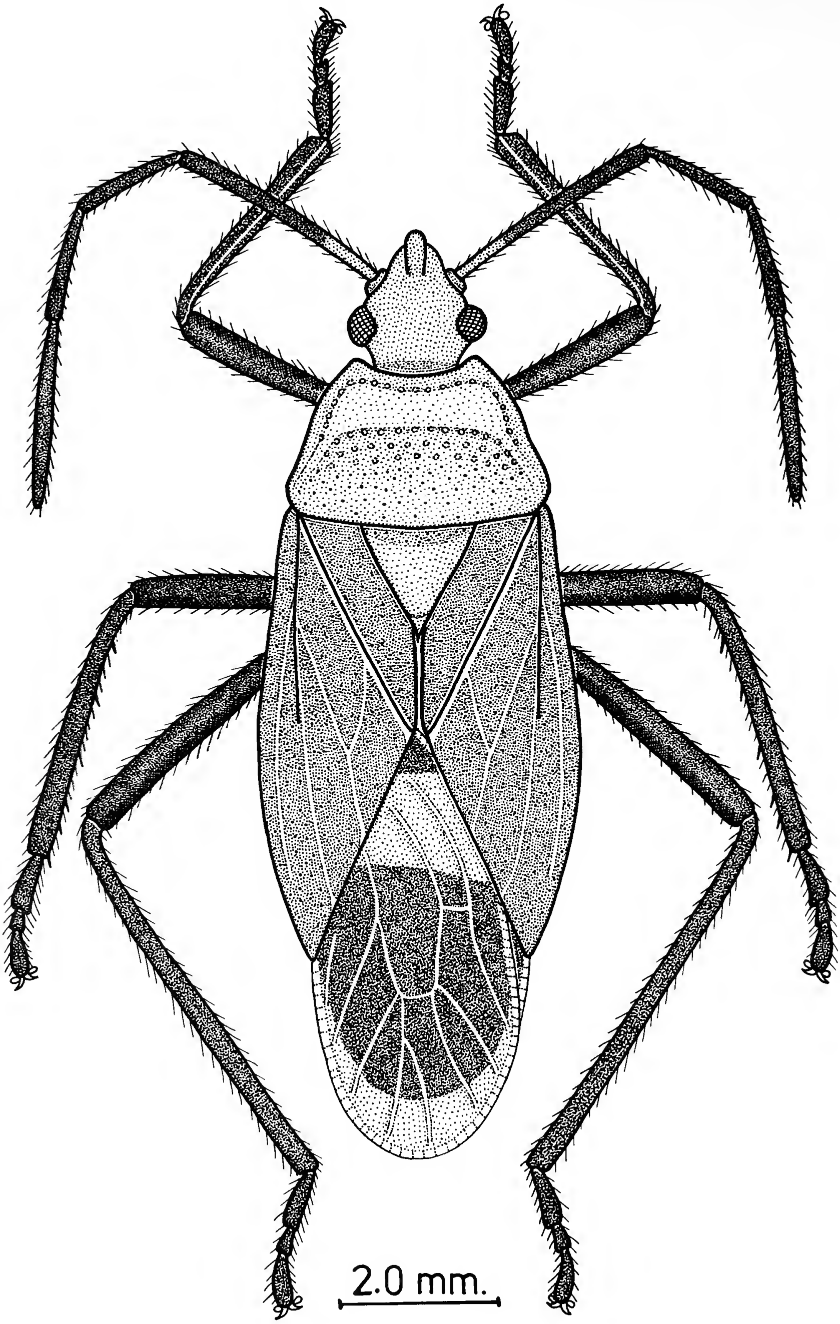
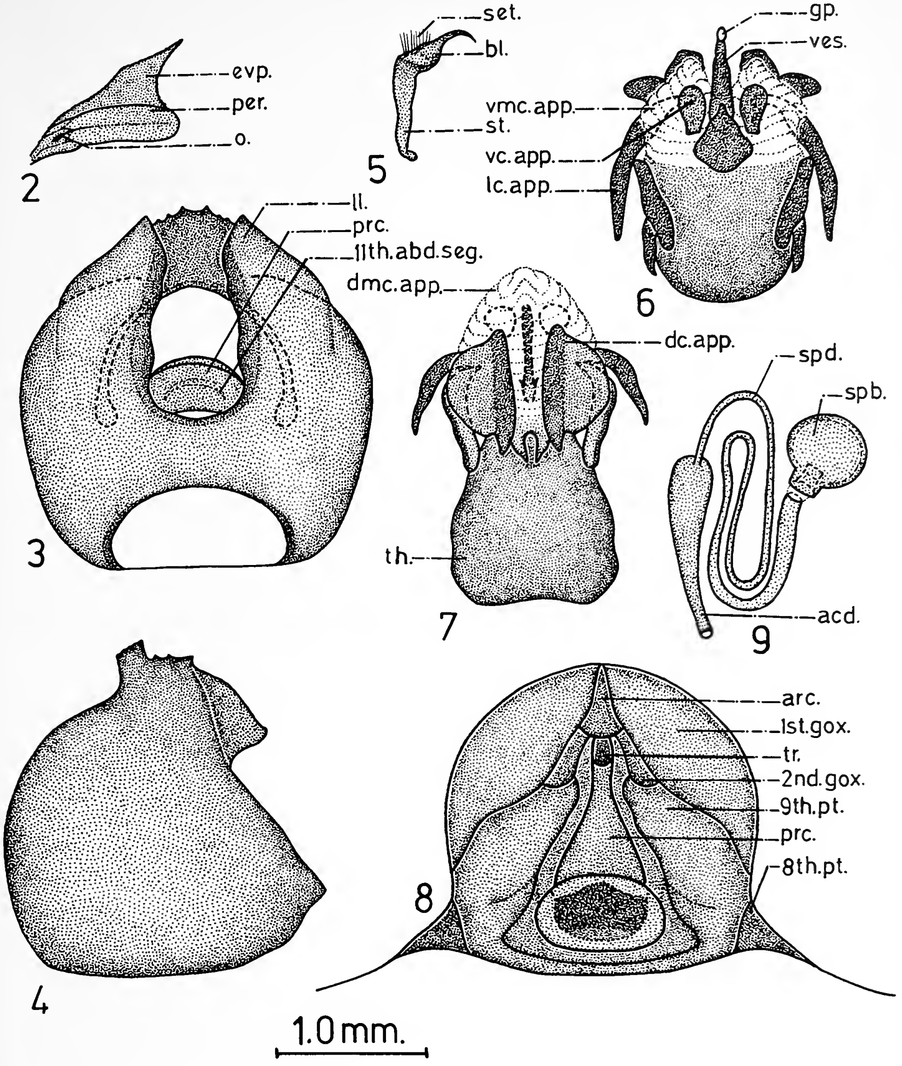


Fig. 1. *F. denticapsulus.* Male, dorsal view.



Figs. 2–9. 2. Metathoracic scent gland ostiole. 3. Pygophore, dorsal view. 4. Pygophore, ventral view. 5. Paramere. 6. Aedeagus, ventral view. 7. Aedeagus, dorsal view. 8. Female terminalia. 9. Spermatheca. 1st. gox. (first gonocoxa); 2nd gox. (second gonocoxa); 8th pt. (eigth paratergite); 9th pt. (ninth paratergite); 11th abd.seg. (eleventh abdominal segment); acd. (accessory duct); arc. (arcus); bl. (blade); dc. app. (dorsal conjunctival appendage); dmc. app. (dorsal membranous conjunctival appendage); evp. (evaporatoria); gp. (gonopore); lc. app. (lateral conjunctival appendage); ll. (Lateral lobe); o. (ostiole); per. (peritreme); prc. (proctiger); set. (setae); sp.b. (spermathecal bulb); spd. (spermathecal duct); st. (stem); th. (theca); tr. (triangulin); vc. app. (ventral conjunctival appendage); ves. (vesica).

In male, pygophore slightly longer than broad, ventroposterior margin denticulate; paramere C-shaped with blade broad proximally and narrowing into sharp spinelike process distally; aedeagus with 4 pairs of conjunctival appendages. In female, first gonocoxae semilunar with posterior margin distinctly sinuate, 9th paratergites about 4 times longer than triangular 8th paratergites; spermatheca with duct and accessory gland fused distally, distal part of spermathecal duct broad.

Type species. Froeschnerocoris denticapsulus, new species.

Discussion. The monotypic genus *Froeschnerocoris* superficially resembles species of *Dysdercus* (Freeman, 1947; Kapur and Vazirani, 1960; Doesburg, 1968), but is distinguished from them in having the anteocular region equal to the posterior length of the head including the eyes, and a denticulate ventrolateral margin of the pygophore.

From an analysis of the pyrrhocoroid genera now in progress, we believe that the features by which *Froeschnerocoris* differs from *Dysdercus* are advanced ones. In addition, the two genera share the following features, which we believe are apomorphic and which suggest the two are sister groups: apical angle of corium elongately acute, incisures of abdominal venter with white bands, and parameres spinelike apically.

Froeschnerocoris denticapsulus, new species
Figs. 1–9

Description. Body pale reddish with brownish punctation, except ⅔ of basal segment and 2nd, 3rd and 4th antennal segments, eyes, legs, a small patch on basal area of membrane and a large patch on distal area of membrane castaneous.

Length of anteocular region equal to length of remainder of head; length of head slightly longer than wide, length of head 1.8–2.4, width 1.7–2.1; 2nd antennal segment only slightly longer than 3rd; length of segments I 2.5–3.2, II 1.5–2.0; III 1.4–1.8; IV 2.4–2.6, antennal formula $3 < 2 < 4 < 1$; basal segment of labium shorter than 2nd, slightly longer than 3rd; length of segments I 1.6–2.2; II 1.9–2.3; III 1.6–2.0; IV 0.9–1.0, labial formula $4 < 3 < 1 < 2$; length anteocular region 0.9–1.2, posterior length of head (including eyes) 0.9–1.2; interocular distance 0.9–1.2.

Width of pronotum slightly more than 1.5 times its length, anterior angles subacute, lateral margins sinuate, length of pronotum 1.9–2.5, width 3.0–4.1; scutellum broader than long, length 1.3–1.8, width 1.4–2.0; ostiolar peritreme with apex broadly rounded, anterior margin convex; distance base scutellum–apex clavus 2.3–3.1; apex clavus–apex corium 2.9; apex corium–apex abdomen (including membrane) 2.3–3.1; apex scutellum–apex abdomen (including membrane) 6.2–8.0. Total length ♂ 11.3–11.4; ♀ 14.2.

In male, pygophore somewhat ovate, dorsoposterior margin deeply concave, ventroposterior margin medially notched, one large and two small denticles on each side, lateral lobe produced into subacute tip, inner surface of ventroposterior margin inwardly directed into subacute apex; inflated aedeagus with pair of dorsal membranous, pair of ventral platelike, pair of bilobed, elongate lateral conjunctival appendages, and pair of medially broad and distally acute dorsal conjunctival appendages.

In female 2nd gonocoxae short, lobelike; proctiger large with posterior margin concave; spermatheca with spherical bulb, flanges not prominent, accessory gland balloonlike.

Holotype. ♂, **India:** Assam, Doom Dooma, May 19, 1943; D. E. Hardy collector (USNM).

Paratypes. ♂, ♀, same data as holotype.

ACKNOWLEDGMENTS

We received financial support from a PARC-USDA Research Project No. FG-Pa-361 (PK-SEA-155). We thank T. J. Henry, A. G. Wheeler, Jr., and C. W. Schaefer for reading the manuscript.

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J. New York Entomol. Soc. 94(2):296–300, 1986

A NEW BURROWER BUG (HETEROPTERA: CYDNIDAE) FROM THE PALEOCENE/EOCENE OF TENNESSEE

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Abstract.—*Paleofroeschnerius magnus* Schaefer, new species, is described from the uppermost Paleocene/Eocene of western Tennessee and assigned to the Cydninae. It is most similar to the modern genus *Ectinopus,* but its cladistic affinities cannot be determined. Its habitat was probably not unlike that of modern cydnines.

A recently investigated uppermost Paleocene/lowermost Eocene fossil locality in western Tennessee is unusual in having many well preserved angiosperm flowers as well as the remains of several insects. Plant families particularly well represented by floral remains include the Leguminosae (Crepet and Taylor, 1985a, b), Euphorbiaceae, Fagaceae, and Juglandaceae. Insect remains include mayfly larvae, various beetles, and the burrower bug described here.

The fossils are preserved as compressions of varying degrees of oxidation in fine-grained clay. The ecological setting is probably a near-shore (the Paleocene "Gulf of Mexico") swamp deposit, as suggested by the stratigraphic geology of the region (Parks, 1975) and a microfossil assemblage that includes the remains of brackish water algae (Zavada, pers. comm.). The age is based on local stratigraphy (Parks, 1975) and on the proportions of juglandaceous palynomorphs in the sediments (Zavada, pers. comm.). These proportions have proven good indicators of age in the Paleogene of the Mississippi Embayment (Frederiksen and Christopher, 1978).

The matrix containing the fossil cydnid has split, so that the dorsal external surface is exposed on the part (Fig. 1A), while the counterpart reveals an internal view (Fig. 1B). The curvature of the abdomen suggests a ventral view, but the presence of connexivum and inner laterotergites indicates a dorsal one. Some parts of the dorsum have been lost, especially of the thorax. Nevertheless, sufficient detail remains to permit subfamily placement and to determine that the specimen represents a new genus.

The bulging forward of the pronotal angles on either side of the head occurs often in the Cydnidae, and much less frequently in other pentatomoid groups. This feature and the bug's general facies place it unequivocally in the Cydnidae (*s.s., nec* Dolling 1981), and suggest it belongs in the Cydninae.

Of the five subfamilies Froeschner (1960) recognized in the Cydnidae, our specimen is excluded from the Amnestinae by its size (present-day amnestines are < 5 mm long), its apparent lack of a claval commissure, and the unequivocal absence of lateral head spines; from the Scaptocorinae by the unmodified, or only slightly modified, foretibiae; from the monobasic Asian Garsauriinae by the much more rounded head; and from the Sehirinae by its greater size and the relationship of head to pronotum.

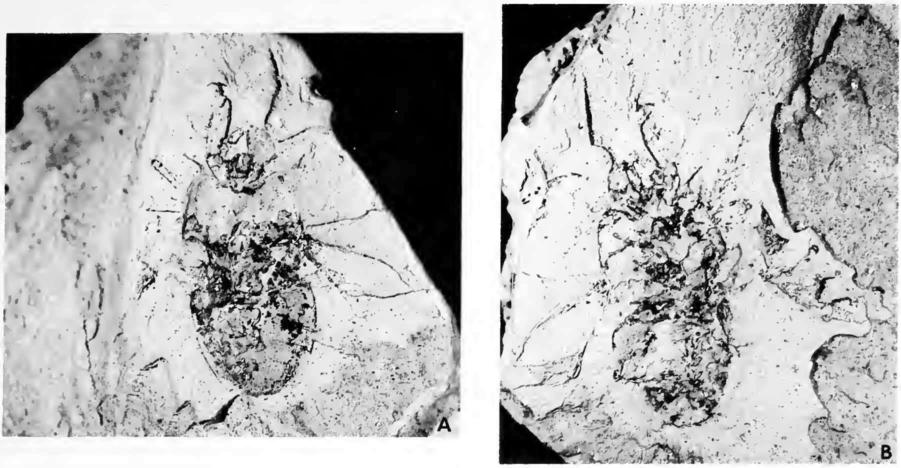

Fig. 1. *Paleofroeschnerius magnus,* dorsal views. 1A, part; 1B, counterpart.

Excluded by these characters from the other four subfamilies, this fossil cydnid can easily be placed in the Cydninae, whose extant members it so closely resembles in general facies.

As we shall argue later, the fossil bug cannot easily be placed in any existing cydnine genus, and we herewith describe the bug as new (Schaefer sole author of the new genus and species).

Paleofroeschnerius, new genus

Description. Large, elongate-oval, widest at prothorax; piceous or black. Head width subequal to length, without lateral spines; juga apparently as long as tylus, jugal-tylar sutures diverging distally. Pronotum much wider than long, much extended forward laterally around head (head thus appearing somewhat withdrawn), without "notch" at humeral angles. Scutellum slightly longer than wide, its tip acute. Without claval commissure. Membranal suture of forewing apparently angled forward posteriorly (artifact?). Foretibiae not greatly modified, with about eight stout bristles laterally. Abdomen with connexival suture to eighth tergite (connexivum complete to eighth tergite); connexival sutures 3–4 probably, 4–5, 5–6, 6–7 certainly present; inner laterotergites present, well developed, with sutures as above. Tip of abdomen (posterior border of eighth tergite) smoothly rounded, suggesting female.

Type species. Paleofroeschnerius magnus, new species.

Paleofroeschnerius magnus, new species
Figs. 1, 2

Description. In addition to the generic features above, and the measurements given below, the following points may be noted: foretibiae apparently slightly thickened, mid-tibiae terete; claws of pro-leg widely divergent. Tergal sutures straight medially, somewhat bowed forward sublaterally.

Measurements (in mm) of holotype. Total length 11.1; head width 2.0, length 1.8;

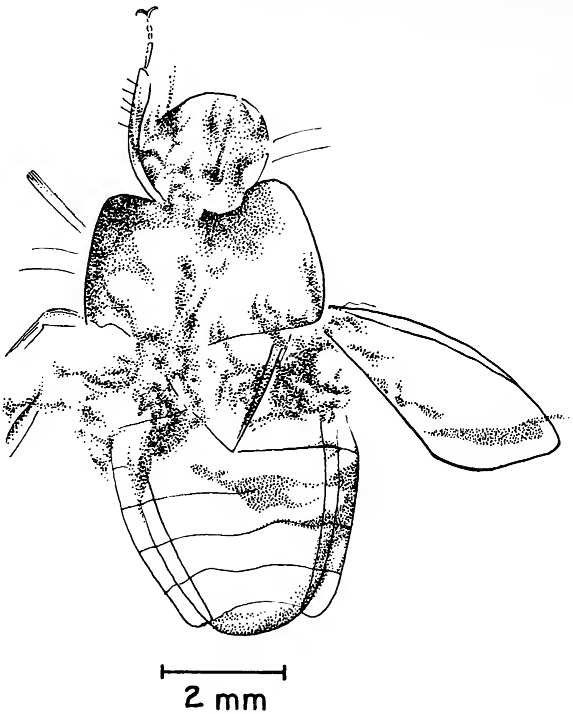

Fig. 2. *Paleofroeschnerius magnus,* dorsal view. Reconstruction, from part and counterpart of Fig. 1. Hindwing and membrane of forewing not shown, being but vaguely discernible.

pronotal width (widest point) 4.9, length 2.7; scutellar width (base) 2.6, length 2.1; foretibial length 1.9; forewing width (widest point; estimate) 2.5, length (estimate) 6.7; hindwing width (widest part; estimate) 3.9, length (estimate) 4.8; claval width (at base) 0.3; abdominal width (widest point) 4.8; connexival width 0.3; inner laterotergite width 0.3.

Etymology. The specific epithet reflects that this bug is somewhat large in the Cydninae. And with the genus we take pleasure in naming the very old in honor of the eternally young: Richard C. Froeschner, doyen of heteropterists.

Depository. The type specimen (two separate parts) will be deposited in the National Museum of Natural History, Washington, D.C.

Discussion. The following features are unique to or unusual in *Paleofroeschnerius magnus* Schaefer: the pronotum bulges forward on either side of the head further than in most (all?) other cydnines. The scutellar tip is sharper than in most. The angling forward of the membranal suture is unusual in Cydninae, although this may be an artifact of preservation.

Of Western Hemisphere cydnine genera, only these contain species of the same size as *Paleofroeschnerius: Cydnus* (the only species, *aterrimus* [Forster], was probably brought to the New World by man), *Cyrtomenus* Amyot and Serville, *Dallasiellus* Berg, *Ectinopus* Dallas, *Onalips* Signoret, *Pangaeus* Stål, *Prolobodes* Amyot and

Serville, and *Tominotus* Mulsant and Rey (Froeschner, 1960). Other cydnines are very much smaller than the fossil.

The somewhat elongate shape of the fossil (length about twice width), even allowing for distortion, excludes it from *Onalips, Tominotus,* and *Prolobodes,* which are in general rounder and more squat. The scutellum of *Paleofroeschnerius* is somewhat wider than it is long (length/width = 0.78), unlike those of *Pangaeus, Cyrtomenus,* and *Dallasiellus,* where length is equal to or greater than width. The fossil's scutellum is not unlike that of *Cydnus aterrimus.* This species, however, has many more than eight protibial spines.

The scutellar tip of *Ectinopus* is sharper than that of many other cydnine genera, yet not so sharp as that of *Paleofroeschnerius.* Overall, however, the latter most closely resembles *Ectinopus* in size, scutellar dimensions and shape, number of protibial spines, and shape of the head.

Paleofroeschnerius also resembles *Melanaethus,* a much smaller genus, in head-shape. This raises the possibility that we have a large fossil representative of a genus whose present-day members are all small. However, the several features unique to the fossil place it clearly in a separate genus. These features, and the combination of those some of which the fossil shares with other genera, also exclude it from any Old World genus with which we are familiar. (In particular, the absence of a notch at the humeral angle excludes it from the Old World *Macroscytus* Fieber a genus which it otherwise in general resembles.) We therefore do not think it likely that the sister group of *Paleofroeschnerius* is to be found in the Old World, despite the likelihood of a North America-Europe land bridge when this cydnid lived (McKenna, 1973; Einarsson, 1964). This cydnid is probably not a member of an Old World-New World species-pair of the sort described in *Gerris* and *Limnoporus* by Schaefer and Calabrese (1980).

This specimen appears to be the first fossil cydnid described from the New World, and perhaps from the Old. Unfortunately, we can learn little about modern groups from it. There is no analysis of the relationships of the cydnid genera. Froeschner (1960) divided the New World ones into two groups, but he based his division chiefly on the metathoracic scent-gland apparatus, a structure unfortunately not preserved in our specimen. As a result, we cannot place *Paleofroeschnerius* relative to other genera, save to say it fits easily into the subfamily and differs in no outstanding way from several other North American genera.

This conclusion is not surprising. The fossil is relatively recent, compared with the probable antiquity of its family, for the Cydnidae appear to be one of the most primitive of pentatomoid families (Schaefer, 1968, 1981). Moreover, the overall similarity of cydnine genera suggests that phyletic change occurs slowly in the subfamily (and, doubtless, in the others of the family).

Cydnines show little host plant preference (Schaefer, unpublished), and *Paleofroeschnerius* cannot be associated with any of the plant groups found with it. The environment was probably a humid one, but the immediate habitat of the cydnid was not necessarily damp; the soils were probably well drained. Therefore, *Paleofroeschnerius magnus* may not have lived in a habitat much different from those of present-day Cydnidae, which are found in, or in the litter on, dry or rather dry soil. It is quite possible, of course, that the insect was washed into this habitat and did not live in it.

ACKNOWLEDGMENTS

We are grateful to I. Ahmad for discussion of the specimen, to M. J. Spring for the drawing, and to G. Feldman for the photography. The work of William L. Crepet was supported by NSF grant No. BSR-8409308.

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BOOK REVIEWS

Revision del genero *Anasa* Amyot-Serville (Hemiptera-Heteroptera-Coreidae-Coreinae-Coreini).—Harry Brailovsky A. Monographias del Instituto de Biologia, Universidad Nacional Autónoma de México, No. 2, pp. 1–266.

For nearly a century, the *Biologia Centrali Americana* has been the primary reference for the heteropteran fauna of Tropical Mexico and Central America. For the most part, only the studies of Harry Brailovsky, of the Instituto de Biologia, Universidad Nacional Autónoma de México, have served as the major supplemental sources of information on terrestrial bugs. (See also review of "Shore Bugs" below.) Brailovsky's latest effort, a revision of the squash bug genus *Anasa,* is his most comprehensive work to date.

Brailovsky's *Anasa* revision is a valuable contribution to the identification of a group well known for its pest species of cucurbits. A key and photographs of all 63 recognized species are given, 18 of which are described as new. Also included for each species is a detailed synonymy, dorsal view illustrations of the head and pronotum, and illustrations of spermathecae, parameres, and the posterior margin of the pygophore. All species are described or redescribed, diagnosed, and distributions given, with museum depositories indicated for the new species. Dorsal view drawings are provided for five species. Brailovsky summarizes the habits of *Anasa* spp., so far as they are known, and provides a brief discussion of the distribution of the group.

In my view, this is one of Brailovsky's finest pieces of work. It is well illustrated, carefully researched, and as easily seen at first glance printed with much higher standards than many of the publications containing Brailovsky's work. Most importantly, however, it represents a revisionary treatment in the best sense, and offers an example for future workers in the Neotropics. I am particularly pleased to see such a treatment in the Coreidae, a group with a taxonomic tradition dating back to Linnaeus and his revisors, but which has been the object of little synthetic or revisionary work in the 20th century.

For anyone interested in the Neotropical bug fauna, this is an invaluable reference. I only hope that it represents one of many more such efforts on the part of Dr. Brailovsky.—*Randall T. Schuh.*

Shore Bugs (Heteroptera, Hemiptera: Saldidae): A World Overview and Taxonomy of Middle American Forms.—J. T. Polhemus. The Different Drummer, 3115 South York, Englewood, Colorado 80110, USA. i–v + 252 pp. $20.00.

It has been said that a Ph.D. dissertation often represents the most original contribution of a given scientist. If this is true, it is also often true that dissertation research is frequently not published, and therefore in the case of systematic work some of the most important contributions are never made available to the scientific community. John Polhemus has avoided the latter circumstance by taking the somewhat unusual step of publishing his own dissertation. Regardless what the method, this is a valuable publication, and with its affordable price should be acquired by anyone interested in the Leptopodomorpha (shore bugs and their relatives) and the evolution of the Heteroptera.

Polhemus includes sections on biology, morphology, character analysis, phylogeny, taxonomy, and zoogeography. All but the taxonomy section are general treatments and not restricted to the middle American fauna. As noted in the introduction, the publication of this volume occurred about seven years after the research was actually completed. Thus, what were original contributions in 1977 have become somewhat more commonplace today—for example, the use of the SEM and the inclusion of cladistic analysis. Nonetheless, even the section on heteropteran phylogenetics contains much useful information, even if some of the conclusions have been reworked and published elsewhere in the meantime. The concept proposed by Polhemus of Leptopodomorpha and Dipsocoromorpha as sister groups has not been accepted by other authors and in my view is not supported by character information. By contrast, Polhemus's generic-level phylogenetic hypothesis for the Saldidae is totally original and only remains to be tested by other workers.

The taxonomy section occupies about one-half of the volume. Two new genera (one for the fossil *Pseudosaldula latah* Froeschner) and five new species are described, and several species are synonymized. Several neotypes and lectotypes are designated. Illustrations of wing pigmentation pattern and genitalic morphology are given for each species, as well as a map detailing distributions in Mexico and Central America. Descriptions or redescriptions are given for all genera and species, as are keys for taxa at all levels.

Polhemus has shed considerable light on the basis for establishing relationships within the Leptopodomorpha, providing a generic-level cladogram for the group. He has also clarified in detail the taxonomy of the Middle American fauna, a project originally undertaken by B. B. Hodgden in the late 1940's, but the results of which for the most part remained unknown. This work will be of lasting value because of its comprehensive character and its attempts at synthesis.—*Randall T. Schuh.*

(Continued from back cover)

Pentatomomorpha

Book Reviews

Journal of the New York Entomological Society

VOLUME 94 APRIL 1986 NO. 2

CONTENTS

Contributions on Heteroptera in honor of Richard C. Froeschner

(*Continued on inside back cover*)

94 JULY 1986 No. 3

Journal

of the

New York Entomological Society

(ISSN 0028-7199)

Devoted to Entomology in General

JOURNAL OF THE NEW YORK ENTOMOLOGICAL SOCIETY

The New York Entomological Society
Incorporating The Brooklyn Entomological Society

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Mailed July 2, 1986

The Journal of the New York Entomological Society (ISSN 0028-7199) is published quarterly (January, April, July, October) for the Society by Allen Press, Inc., 1041 New Hampshire, Lawrence, Kansas 66044. Second class postage paid at New Brunswick, New Jersey and at additional mailing office.

Known office of publication: American Museum of Natural History, New York, New York 10024.

Journal of the New York Entomological Society, total copies printed 850, paid circulation 700, mail subscription 700, free distribution by mail 18, total distribution 718, 132 copies left over each quarter.

J. New York Entomol. Soc. 94(3):303–330, 1986

CLADISTICS OF THE CHRYSIDOIDEA (HYMENOPTERA)

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Abstract.—A cladistic analysis of the relationships of the families of the Chrysidoidea is presented, and contrasted with the efforts of previous authors. The phylogenetic system here proposed is: Plumariidae is the sister-group of the other six families, which together form a monophyletic group. Scolebythidae is the sister-group of ((Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae)). Embolemidae and Dryinidae are sister-groups, and the closest relative of this component is the Sclerogibbidae. Bethylidae and Chrysididae are sister-groups, and together are the sister-group of Sclerogibbidae + (Embolemidae + Dryinidae). The monophyly of each of the families is established.

Even recently, it has been common to state that no clear line can be drawn between Aculeata and the parasitic Apocrita (e.g., Malyshev, 1968; Evans and Eberhard, 1970; Richards and Davies, 1977). Traditional morphological *differentiae* such as trochanters one or two segmented, and hind wing jugal (sometimes termed anal) lobe present or absent are not consistently distributed. Even the sting has been stated to still function as an ovipositor in some of the aculeate families (e.g., Richards and Davies, 1977). This is scarcely possible given its anatomy, but the sting remained unstudied until recently in several key families. Discussion of the differences between the Parasitica and Aculeata has usually concentrated on behavior, with the Aculeata regarded as comprising mostly predatory forms. Thus the placement—and even composition—of the parasitic chrysidoid families has fluctuated between Parasitica and Aculeata in general treatments (e.g., Riek, 1970; Richards and Davies, 1977).

However, the adoption of cladistic methods has had a tremendous impact on ideas of phylogeny in the Aculeata. Oeser (1961), in a detailed phylogenetic study of the hymenopteran ovipositor, not only clearly established the monophyly of the Aculeata, but also identified a synapomorphy for Bethylidae + Chrysididae and showed a sister-group relationship between this group and the remainder of the Aculeata. This was followed by Brothers' (1975) analysis of 25 family-level taxa of Aculeata (cf. his fig. 2). While concentrating primarily on the Scolioidea *auct.*, Brothers provided the first detailed cladogram of the stinging Hymenoptera, and so put all subsequent investigations on a firm foundation. This is reflected in the works of Koenigsmann (1978) and Rasnitsyn (1980). Both these authors discussed the evolutionary relationships of the entire Hymenoptera, but, influenced by Brothers, treated Aculeata in greatest detail and presented their thoughts as critiques of his system. Both had substantial disagreements with Brothers, but none of these workers completely resolved the relationships of the chrysidoid families.

I have reanalyzed the relationships of the families of this group, and have reached different conclusions from previous authors. These results are summarized in Figure

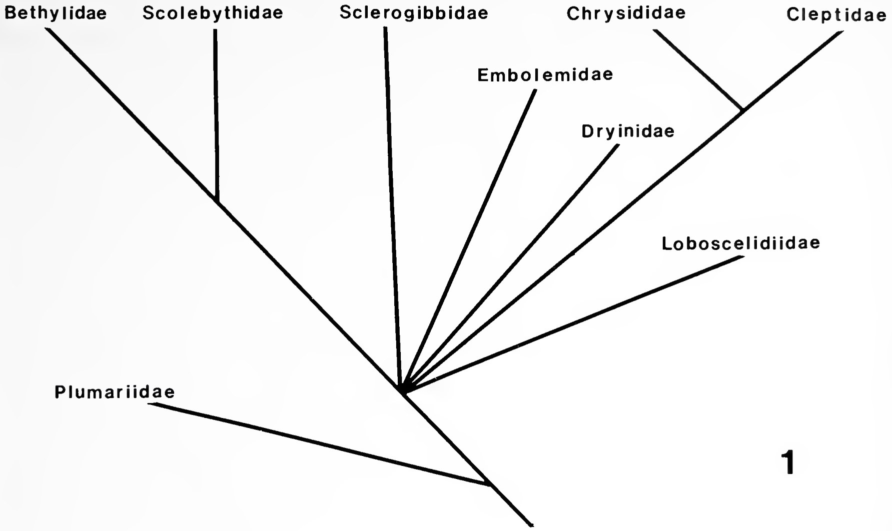
4. Below I present a brief summary of the recent systems suggested for the Chrysidoidea, followed by the diagnoses (apomorphies; see Farris, 1979) for my cladogram, and discussion of the characters. This is the first complete cladistic analysis of the relationships among chrysidoid families.

RECENT HYPOTHESES

Brothers (1975) did not examine all the chrysidoid families. He considered Plumariidae and Scolebythidae separately, and lumped Bethylidae, Chrysididae, Cleptidae (a subfamily of Chrysididae, cf. Krombein, 1957; Day, 1979; Bohart and Kimsey, 1982) and Dryinidae into a "bethylid group" in his analysis. He stated that Sclerogibbidae, Embolemidae and Loboscelidiidae (a subfamily of Chrysididae, cf. Day, 1979), which he did not see, were considered to belong to the bethylid group. His cladogram for the taxa he actually studied (1975:fig. 2) placed Plumariidae as the sister-group of Scolebythidae + the "bethylid group." However, his figure 67, including all the aculeate families, showed Scolebythidae and Bethylidae as sister-groups, placing the remaining "bethylid group" families in an unresolved polychotomy. This is reproduced here as Figure 1. Brothers' legend (1975:588) indicated that these relationships within the Chrysidoidea (termed by him Bethyloidea) were based on "personal impressions."

Koenigsmann (1978) presented essentially a critical literature review. He followed principles of phylogenetic reasoning, but did not himself examine specimens of all the taxa. Consequently he was unfamiliar with some of the characters, which resulted in occasionally superficial treatment. He removed Sclerogibbidae from the Chrysidoidea and placed it as the sister-group of the entire Aculeata, primarily based on heavily weighting 13-segmented antennae. This was the only synapomorphy for his Aculeata, and of course implied that the multisegmented antennae of sclerogibbids was the primitive condition. He pointed out that possession of the crucial autapomorphies of the Aculeata, the sting characters, remained to be demonstrated for sclerogibbids, but averred that they could not be placed in the Parasitica. He alluded to the possibility of the multisegmented antennae of the Sclerogibbidae being secondary, and mentioned in passing the similarity of the wing venation groundplans of this family and the Chrysidoidea (termed by him Bethyloidea). Koenigsmann's suggested relationship represents a radical departure from the tradition, extending back to Ashmead (1902) and Kieffer (1914), of considering Sclerogibbidae as close to Bethylidae. Within this restricted Chrysidoidea, he depicted the relationships as mostly unresolved (see Fig. 2), but did indicate the following sister-groups: Embolemidae + Dryinidae (based on 10-segmented antennae and a tibial spur formula of 1-1-2), Chrysididae + Cleptidae (various characters, including the tubelike ovipositor) and Scolebythidae + Plumariidae (based on absence of a pronotal collar, a character mentioned by Brothers, 1975).

Rasnitsyn (1980), by contrast, provided some new data. He rejected cladistics (terming it a "sterile trend" on p. 7 of the original text), and proceeded largely by attempting to draw smooth transitions between taxa (for example, his discussion of the placement of Miomoptera on p. 38 of the original). This is unsurprising given his paleontological background, but at least he dealt with characters to the extent



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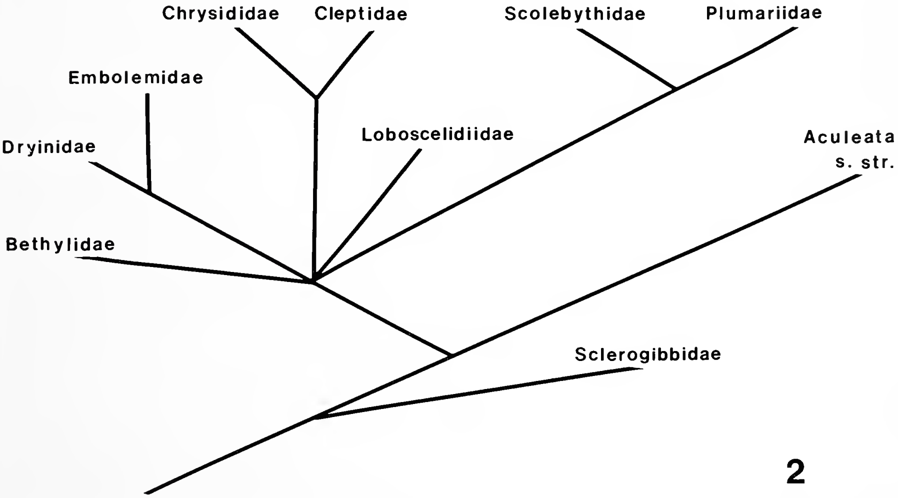

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Figs. 1, 2. 1. Cladogram of the Chrysidoidea, after Brothers (1975:fig. 67). 2. Cladogram of the Chrysidoidea, after Koenigsmann (1978:fig. 4).

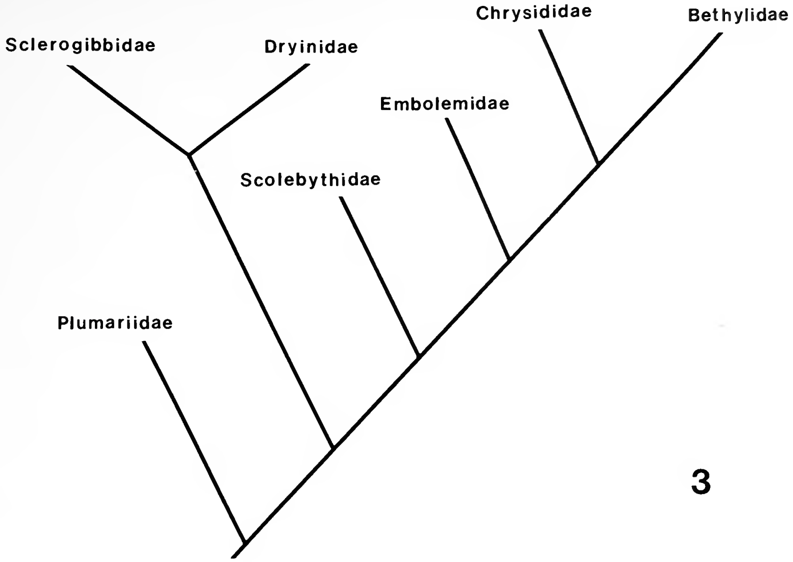
that he rejected some of Brothers' and framed his discussion of aculeates in terms of alternative character interpretations. He figured (1980:fig. 147f) the first dissection of the sting of a sclerogibbid, as well as illustrating stings of the other chrysidoid families (except Plumariidae). His cladogram (here as Fig. 3) grouped Bethylidae + Chrysididae, based on the loss of the articulation between the second valvifer and second valvulae of the sting, as first noted by Oeser (1961). But he then grouped Embolemidae as the sister-group of this component. He first stated that the antennae of embolemids and dryinids were different in structure (not geniculate and scape long vs. "often" geniculate and scape short; pedicel/flagellum articulation fixed vs. mobile). He dismissed the shared homopteran hosts by arguing that the host habitats were different, and that the "confined" hosts of embolemids were similar to those of Bethylidae + Chrysididae in habitat. He stated that the endoparasitism of embolemids (Bridwell, 1958) found its "analogy among Aculeata only in Chrysididae." Finally, he noted that embolemids and dryinids both lacked a furcula in the sting, but considered the elongate base of the second valvulae in Embolemidae, which is compressed into a vertical lamella (Rasnitsyn, 1980:fig. 147b), to resemble the unpaired part of the furcula in Bethylidae and perhaps to be homologous with it.

Besides these arguments, he advanced two characters as synapomorphies for Embolemidae + (Bethylidae + Chrysididae). These were the metasternum and the articulation between metasomal sterna I and II. He considered the metasternum of Bethylidae to be derived (Brothers, 1975, treated it as plesiomorphic in Aculeata) and the median carina of embolemids and chrysidids to be either a precursor or rudiment of it. He characterized the articulation between metasomal sterna I and II in these three families as with a "primarily" thick, straight margin to I (secondarily with membranous lobes and median notches in Chrysididae); and a straight margin to II, with small lateral notches and edges invaginated with desclerotized areas (notches and desclerotized areas large and edges little invaginated in Chrysididae).

Among the remaining families, he suggested a sister-group relationship between Sclerogibbidae and Dryinidae. This was supported by: 1) metasomal sternum II with median notch and expanded acrosternite; 2) elongate base of the second valvulae, although "the process thus formed differs in shape"; 3) enlarged foretarsal claws in the female (he noted that only one unguis was enlarged in only some dryinids, so this was "a common tendency"); 4) ectoparasitism of active non-Holometabola hosts. He characterized the Scolebythidae and Plumariidae as "the earliest groups to diverge off the common stem of Chrysidoidea," but did not draw any conclusions about which came off first or the relationships of his four main chrysidoid components to one another (although his cladogram was completely resolved; here as Fig. 3). It will be shown below that most of Rasnitsyn's conclusions are not tenable.

GROUNDPLAN DIAGNOSES

This section lists the *inferred* autapomorphies for each component and term (*sensu* Nelson, 1979: components are branch points and terms are terminal taxa) of the cladogram of Figure 4. The states are those of the groundplan of each group, and may have been further modified in individual members of a component or term. Justification of these interpretations is deferred to the following section, along with



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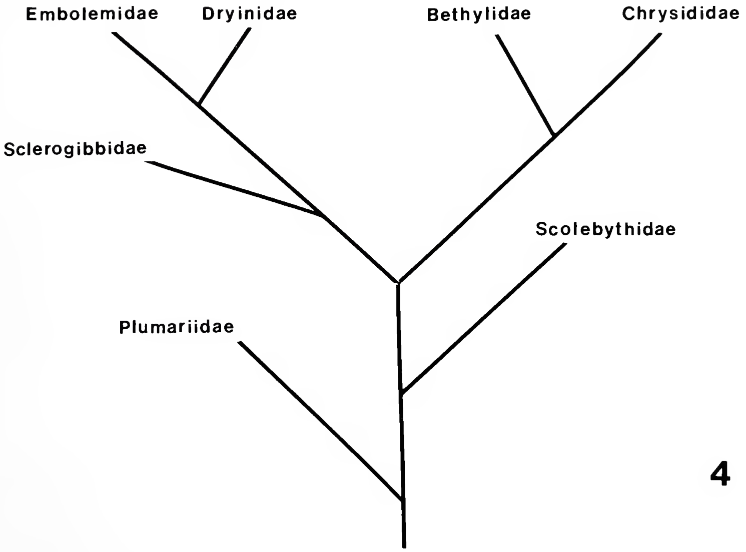

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Figs. 3, 4. 3. Cladogram of the Chrysidoidea, after Rasnitsyn (1980:fig. 38). 4. Cladogram of the Chrysidoidea, according to the present work.

discussion of characters mentioned by previous authors but not found to be useful in this study.

Chrysidoidea Latreille, 1802

Reduction in venation: fore wing with eight cells (third discoidal and third submarginal lost by reduction of m-cu_2 and r-m_3). Hind wing with veins 2A, 3A and jugal lobe lost.

Loss of metathoracic-propodeal suture ventral to the endophragmal pit.

Articulation within the second valvifer of the sting.

Plumariidae Brues, 1924 (1914)

Palpal formula 6:3 (5:3 in females).

Prosternum with posterior surface depressed.

Male metasternum entirely depressed below level of mesosternum.

Female wingless, pronotal collar reduced, and mesosoma modified in connection with aptery.

Scolebythidae + ((*Sclerogibbidae* + (*Embolemidae* + *Dryinidae*)) + (*Bethylidae* + *Chrysididae*))

Fore wing with seven closed cells (loss of second submarginal due to loss of r-m_2), RS_2 vein lost.

Hind wing venation reduced: all cells, all crossveins and M+Cu vein lost.

Scolebythidae Evans, 1963

Prosternum enlarged.

Pronotal collar reduced.

Forecoxae posteriorly produced.

(*Sclerogibbidae* + (*Embolemidae* + *Dryinidae*)) + (*Bethylidae* + *Chrysididae*)

Palpal formula 6:3.

Metapostnotum constricted.

Sclerogibbidae + (*Embolemidae* + *Dryinidae*)

Hind wing with veins SC+R+RS and 1A lost.

Furcula lost, elongate base of second valvulae forming lamellate process.

Sclerogibbidae Ashmead, 1902

Antennae with more than 14 segments.

Palpal formula 5:3.

Female wingless, with subcordate head and fore femora enlarged.

Hosts Embiidina.

Embolemidae + *Dryinidae*

Fore wing with six closed cells (first submarginal lost due to reduction of RS).

Antennae 10-segmented.

Loss of one mid-tibial spur.

Hosts Homoptera Auchenorrhyncha.

Endoparasitic in first instar and later protruding from host.

Embolemidae Foerster, 1856
Antennal prominence.
Female palpal formula 4:2.
Fore tibial calcar strongly curved and truncate.

Dryinidae Haliday, 1833
Fore wing with five closed cells (loss of discal cell due to reduction of m-cu_1 and RS+M).

Bethylidae + *Chrysididae*
Loss of articulation between second valvulae and ventral part of second valvifer.

Bethylidae Haliday, 1839
Head capsule modifications associated with prognathy.
Clypeus with longitudinal median carina.
Metasternum anteriorly broad.

Chrysididae Latreille, 1802
Fore wing with six closed cells (first submarginal lost due to reduction of RS).
Palpal formula 5:3.
Female with four visible metasomal terga, male with five.
Type of articulation between metasomal sterna I and II.
Ovipositor tube.

CHARACTER ANALYSIS

The wings

The wing venation has not generally been used in the higher-level taxonomy of the Chrysidoidea. Brothers (1975) considered the reduction in the number of cells in the hind wing to be "probably significant" in associating Scolebythidae with his "bethylid group," and loss of the hind wing jugal lobe has long been used as a distinguishing feature of the superfamily. But aside from this, the wings have probably been considered more often a source of difficulty than a source of characters. This is due to apparently similar patterns of reduction appearing in many groups (including other Hymenoptera), a situation that traditional taxonomy is ill-equipped to deal with. When cladistic analysis, with its emphasis on similarity in groundplans, is applied to the venation, a more coherent pattern emerges.

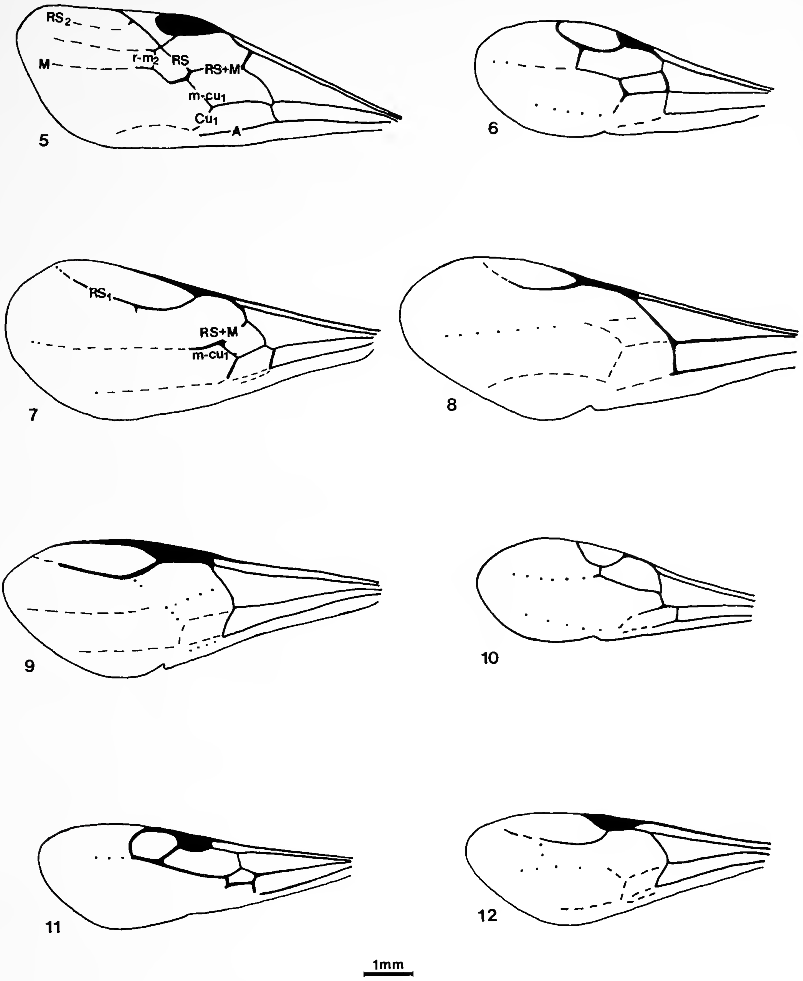
In this discussion, only convex, pigmented veins are treated. In many of the instances of extensive reduction, the veins may be indicated by traces, that is unpigmented lines or creases. The term "reduced" is used to indicate veins reduced to such traces or completely lost. In the terminology of Mason (1986a), these traces are "spectral" veins, which may evanesce over their course. Mason (1986a) recognized two other, prior stages in the reduction of convex, pigmented veins: "tubular" for those with sharply defined edges, and "nebulous" for those with ill-defined edges. Nebulous veins are here considered as not reduced. However, it should be noted that the transition to spectral veins may be gradual.

Fore wing. The groundplan number of closed cells in the fore wing of Aculeata is considered to be ten (Brothers, 1975). This is the number in the Aculeata s. str. (Sphecoidea + Vespoidea, *sensu* Brothers, 1975), the sister-group of the Chrysidoidea. The evolution of the venation in chrysidoids is a history of progressive reduction from this plesiomorphic state. The maximum number of cells in the Chrysidoidea is eight, found in the Plumariidae (Fig. 5), which may be inferred to be the groundplan condition in the superfamily. As such, it is an autapomorphy of the group. This state is a product of the loss of the m-cu_2 and r-m_3 crossveins, compared to the sister-group, which results in the loss of the third discoidal (2M) and third submarginal (2RS) cells, respectively.

All Chrysidoidea, aside from Plumariidae, also lack the second submarginal cell (1RS), due to the loss of the r-m_2 crossvein (Figs. 6–12). Further, they lack the RS_2 vein, present as a spur on the marginal cell in plumariids (Koenigsmann, 1978, and Rasnitsyn, 1980, considered this an apomorphic *de novo* vein; Day, 1977, adopted the interpretation followed here). These states are therefore synapomorphies of the six families. From this condition there has been further extensive reduction, ranging to only one closed cell (in aphelopine dryinids, Loboscelidiinae and some bethylids). However, the pathways of reduction have been different in most of the groups and the resultant patterns differ in detail.

Embolemids and chrysidids have six cells in the groundplan (Figs. 7, 8). They lack the first submarginal cell due to reduction of the RS vein. This is also true of dryinids, but that family has only five cells in the groundplan (Fig. 9); they lack also the discal (1M) cell, due to the loss of the m-cu_1 crossvein and reduction of the RS+M vein. In those dryinids with apparent RS and m-cu_1 these are spectral veins (Fig. 9; some *Deinodryinus,* where RS may appear nebulous in part; *Thaumatodryinus*). Reduction to six cells by loss of the first submarginal is here interpreted to be a synapomorphy of the Embolemidae + Dryinidae, with further loss of the discal cell an autapomorphy of the Dryinidae. The state of reduction of the first submarginal cell is also found in Chrysididae as a groundplan character. This must be inferred to be convergent, as both sclerogibbids (Fig. 10) and some bethylids have this cell (Bethylinae: Fig. 11, *Eupsenella,* where it is closed by tubular veins; in *Lytopsenella,* it is closed by nebulous veins, cf. Evans, 1964). Other bethylids (including Mesitiinae) have RS+M and m-cu_1 reduced to spectral veins or completely lost, and so the question arises as to whether the appearance of these veins in bethylines is secondary. However, Evans (1964) treated bethylines as relatively primitive (cf. his fig. 1), and thus the interpretation of presence of the first submarginal in the bethylid groundplan under present knowledge is better supported.

From these states further reductions have occurred within families, but as they do not pertain to the groundplans they are not important for family level relationships. The Cu_1 and A veins are nebulous in most groups (Figs. 6–10, 12), and may be distally reduced so that the second discoidal cell appears open (Figs. 5, 6, 8). This state also occurs in the plumariid *Myrmecopterinella* (Day, 1977), which has additionally lost the second submarginal cell. The marginal cell is closed only by a distally nebulous RS_1 vein, which may become spectral, in many groups (Figs. 7–9, 12). Although the groundplan state in dryinids is five closed cells, most species have fewer. The second discoidal, submedian (M+Cu_1) and median (R) cells may be lost and



Figs. 5–12. Fore wings of Chrysidoidea. 5. *Plumarius* (Plumariidae). 6. *Ycaploca evansi* (Scolebythidae). 7. *Embolemus* (Embolemidae). 8. *Cleptes semiauratus* (Chrysididae). 9. *Tridryinus poecilopterae* (Dryinidae). 10. *Sclerogibba* (Sclerogibbidae). 11. *Eupsenella* (Bethylidae). 12. *Pristocera armifera* (Bethylidae). ——: tubular vein; — — —: nebulous vein; · · · · ·: spectral vein.

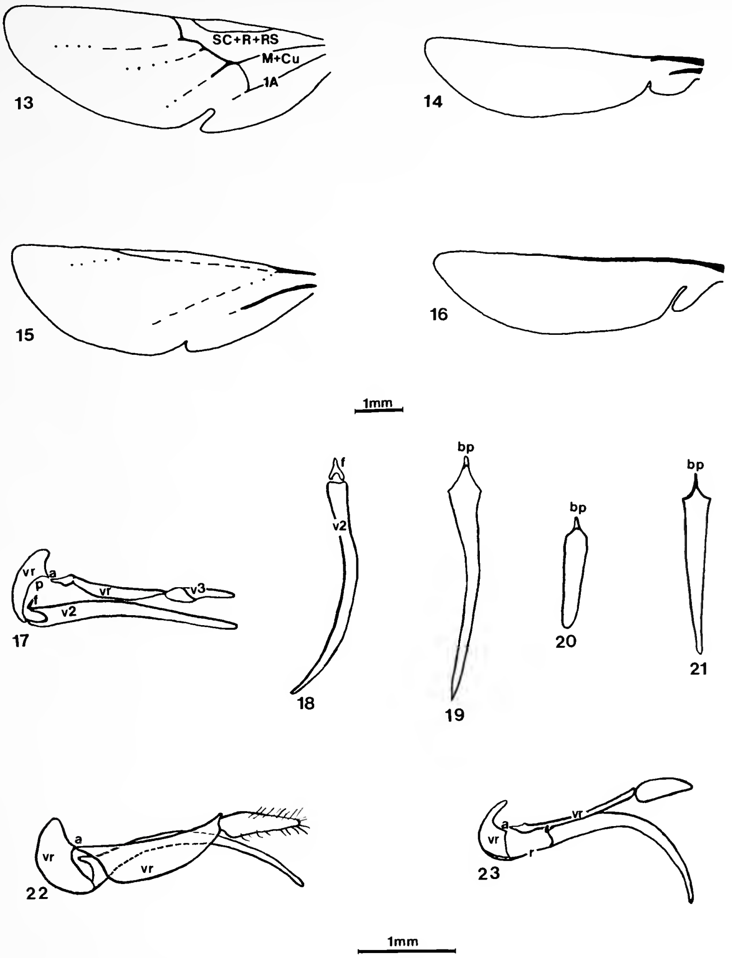
the marginal cell may be open (cf. Olmi, 1984). The discal cell is absent in the sclerogibbid *Probethylus,* as well as some species of *Sclerogibba* (Fig. 10). Many chrysidids have only three cells closed by tubular or nebulous veins; the marginal cell is open and the discal and second discoidal cells are lost. In *Loboscelidia* only the median cell is closed. Finally, no bethylid actually has seven closed cells. The marginal cell is often open, and the first submarginal, discal and second discoidal cells absent. The first submarginal and discal cells are present only in some Bethylinae (Fig. 11) and the second discoidal cell closed, by nebulous veins, in Pristocerinae (Fig. 12). One or two closed cells occurs in Epyrinae.

Hind wing. The primitive number of cells in the hind wing of Aculeata is three (Brothers, 1975), the number found in Sphecoidea + Vespoidea, and Ichneumonoidea, the sister-group of the Aculeata (Mason, 1986b). Veins 2A and 3A are present in addition to a jugal lobe (Brothers, 1975). All Chrysidoidea lack veins 2A and 3A and the jugal lobe. These developments are autapomorphic in the superfamily, although they have occurred elsewhere in the Aculeata (Brothers, 1975). Rasnitsyn (1980) questioned whether absence of a jugal lobe in chrysidoids was not actually plesiomorphous, "since Karatavitidae are so far the only Jurassic forms of the Apocrita in which the jugal lobe has been found, and we have no grounds to assume its presence in the ancestor of the Aculeata." On the contrary, since a jugal lobe is found also in Symphyta (and veins 2A and 3A) and Evanioidea, there is certainly reason to consider its presence in Aculeata (a relatively primitive group of Apocrita; Mason, 1986b) as plesiomorphic.

Compared to Plumariidae (Fig. 13), the remaining Chrysidoidea have derived hind wing venation. All crossveins and vein M+Cu are lost. The costa is distally reduced, and SC+R+RS and 1A are the remaining longitudinal veins (Fig. 14). There are no closed cells, except for the costal in some Chrysididae (Fig. 15). Brothers (1975) treated this presence as the primitive condition in his "bethylid group," but it is here considered as a secondary reversal in chrysidids. This is the parsimonious interpretation, for if it were plesiomorphic in Chrysidinae then the costal cell must be inferred to have been convergently reduced at least nine times (scolebythids, sclerogibbids + embolemids + dryinids, bethylids, Cleptinae, Amiseginae + Loboscelidiinae, Elampinae, Parnopinae, Allocoeliinae and within Chrysidinae; cf. Bohart and Kimsey, 1982:fig. 1, for a cladogram of chrysidid subfamilies). The case for reversal is therefore strong. A similar interpretation is here applied to the M+Cu vein (only *distally* tubular) present in a few Chrysidinae (*Stilbum*) and Cleptinae (distally nebulous, Fig. 15).

From the inferred primitive longitudinal vein complement of SC+R+RS, 1A and a distally reduced C, the Sclerogibbidae + (Embolemidae + Dryinidae) are further derived in lacking SC+R+RS and 1A (Fig. 16). This is a synapomorphy of these families. SC+R+S has also been distally reduced in some Bethylidae + Chrysididae.

Brachyptery. Reduction or loss of the wings has occurred numerous times in the female sex in Chrysidoidea. Males are sometimes micropterous (Dryinidae, see Olmi, 1984; Bethylidae, Evans, 1964) or apterous (Chrysididae, Krombein, 1957). That these are independent is attested to by the different modifications of the mesosoma associated with brachyptery in the different groups (reviewed by Reid, 1941, and see Evans, 1966, and Brothers, 1975). Brachyptery is characteristic of female Plumariidae and Sclerogibbidae. It is autapomorphic in each of these groups. Reid (1941) stated that all female Embolemidae are brachypterous or short-winged, but fully winged females occurr in *Ampulicomorpha confusa* as well as various undescribed species. It is also found in some Dryinidae (within Anteoninae, Bocchinae, Gonatopodinae



Figs. 13–23. 13–16. Hind wings of Chrysidoidea. 13. *Plumarius* (Plumariidae). 14. *Eupsenella* (Bethylidae). 15. *Cleptes semiauratus* (Chrysididae). 16. *Embolemus* (Embolemidae). 17. *Clystopsenella longiventris* (Scolebythidae). Lateral view of sting apparatus. Tergum IX, first valvifer and first valvulae not shown. 18–21. Oblique ventral view of second valvulae (sting). 18. *Plumarius* (Plumariidae). 19. *Probethylus callani* (Sclerogibbidae). 20. *Ampulicomorpha confusa* (Embolemidae). 21. *Tridryinus poecilopterae* (Dryinidae). 22–23. Lateral view of sting apparatus. 22. *Probethylus callani* (Sclerogibbidae). 23. *Pristocera armifera* (Bethylidae). a: articulation between dorsal and ventral arms of second valvifer; bp: basal process of second valvulae; f: furcula; p: postincision; r: ramus of first valvula (lancet); v2: second valvulae (sting); v3: third valvulae (gonostylus); vr: second valvifer.

and Apodryininae), Bethylidae (within each subfamily) and Chrysididae (within Amiseginae). In itself, it is evidently not significant, nor are the associated modifications generally even family characters.

Head

Head shape. The most distinctive aspect of the bethylid facies is prognathy. Its appearance in the female has been used as the key character of the family (Koenigsmann, 1978), although Mesitiinae are then considered a problem, as they are stated to be orthognathous (Moczar, 1970; Koenigsmann, 1978; Nagy, 1969 actually termed them hypognathous!). This character has not been studied carefully. There is variation in the trait; it is exaggerated when the head is elongate, as in *Pristocera* females. The genal bridge (found throughout Chrysidoidea) is expanded, and ventrally comprises half or more the length of the head. The postgenal bridge is also expanded, and is often still separated from the genal bridge by the occipital carina. The temples and upper face are lengthened relative to the rest of the head, and the proboscidial fossa shortened in the extreme condition. The eyes are usually situated very close to the mouthparts, and occupy relatively little of the lateral surface area of the head, typically less than half the length of the head capsule, and may be greatly reduced in genera such as *Pristocera.* The elongation of the genal and postgenal bridges, and the relatively small eyes obtain regardless of the orientation of the mouthparts, which is a relatively unimportant feature. Due to these characters most bethylids are prognathous to some extent—including males and Mesitiinae. To be sure, the development of "prognathy" in the females of the subfamilies Pristocerinae, Epyrinae and Bethylinae is usually greater than that in males and Mesitiinae, but is a matter of degree and does not appear in all species. For example, in *Goniozus* the eyes are larger relative to the rest of the head, and the mouthparts less prognathous than Mesitiinae. For present purposes it is enough to establish that Bethylidae are apomorphic in their type of head capsule relative to the rest of the Chrysidoidea, particularly the cleptine and amisegine chrysidids, to which Mesitiinae have often been likened (Ashmead, 1902; Reid, 1941; Nagy, 1969; Moczar, 1970). In chrysidids, the genal bridge is often similarly elongate, although the mouthparts are orthognathous. The postgenal bridge is not so elongate, but the most significant difference compared to bethylids is that the eyes cover most of the lateral surface of the head—the temples are practically nonexistent. In general other Chrysidoidea have the eyes relatively larger than in bethylids. The female plumariid I have seen has relatively small eyes and a broad genal bridge with prognathous mouthparts, but the postgenal bridge not so well developed. The eyes may be relatively small and the mouthparts somewhat prognathous in scolebythids (*Ycaploca,* where the head in lateral view even appears to have the oblong shape characteristic of the highly derived bethylids). But the genal bridge is not so broadened and the proboscidial fossa is larger. The mouthparts are somewhat prognathous in sclerogibbid females and some dryinids, but again the details of the head shape are different. Sclerogibbids have rather elongate eyes and the postgenal bridge not well delimited, and dryinids have the eyes relatively larger and the hypostoma enlarged when prognathous. The genal bridge is not as broad, and this is also true in embolemids, where the eyes may be relatively small.

There are thus numerous modifications of the head shape, and each of the chrysidoid families could perhaps be said to have some apomorphies. The orientation of the mouthparts *per se* is not important. A broad genal bridge is common, but bethylids are unique in combining that with a broad postgenal bridge and primarily relatively small eyes—and often with prognathous mouthparts. Mesitiinae are not similar to Chrysididae in head characters, and as discussed below, are only superficially similar in other features. Among the remaining families, the sclerogibbids have the most outstanding apomorphy: the subcordate female head (figs. in Krombein, 1979). The posteriad projection of the vertex, bordered by broad flattened setae (Krombein, 1983), in Loboscelidiinae is also remarkable.

Clypeus. In the Chrysidoidea the clypeus is usually quite short and transverse, a state Brothers (1975) concluded is primitive in Aculeata. Bethylidae have an autapomorphy of the clypeus: a longitudinal basomedian carina. The length and height of the carina vary (figures in Evans, 1978); it may be continuous with a frontal carina proceeding dorsad of the antennae (e.g., *Goniozus*) or laterally dilated (*Mesitius apterus,* fig. 11 in Moczar, 1970). It is absent secondarily in some epyrines and bethylines (e.g., figs. in Evans, 1978), but is present in the great majority of taxa. The clypeus is variously modified in chrysidids but not carinate. A *frontal* carina is present in some amisegines (*Alieniscus,* Krombein, 1957) but in general the front is excavated in chrysidids.

Antennae. Characters of the antennae have played a prominent role in discussion of the taxonomy of Chrysidoidea. In particular, the number of segments has been frequently discussed. Sexual dimorphism in the antenna segmentation is an autapomorphy of the "Aculeata s. str." (Brothers, 1975; Koenigsmann, 1978; Rasnitsyn, 1980). The 12-segmented antennae in the female is considered a reduction from 13 segments, found in males and most Chrysidoidea (as well as many Parasitica). The groundplan number of 13 segments is in turn a reduction from the multisegmented antennae of other Macrohymenoptera (Ichneumonoidea, the sister-group of Aculeata; Mason, 1986b). The Sclerogibbidae are then a problem, for their antennal segment number ranges from 15 (a female *Probethylus* from Texas I have seen) to 39 (Richards, 1958). Koenigsmann (1978) therefore placed this family as sister-group to the entire Aculeata. However, the number of segments varies not only between and within sexes of the same species (Richards, 1939b; Shetlar, 1973; Krombein, 1979; pers. obs.) but within the same individual (Richards, 1939b). This instability can be considered to provide support for the interpretation of secondary increase, and reversal is required in any event in view of the chrysidoid autapomorphies that sclerogibbids possess (contrary to Koenigsmann, 1978).

The number of segments has not only increased during the evolution of the Chrysidoidea, it has decreased in some groups. The number is 12 in both sexes of some bethylids (Evans, 1964) and at least the male of *Myrmecopterinella* (Plumariidae; Day, 1977). And the number is 10 in both sexes of Embolemidae + Dryinidae. This state is usually taken to indicate recent common ancestry for these two families (Koenigsmann, 1978), however Rasnitsyn (1980) considered the number to be convergent. He stated that the antennae in these two families were markedly different in structure, often geniculate and with a short scape and mobile pedicel/flagellum articulation in Dryinidae vs. not geniculate and with a long scape and fixed pedicel/flagellum articulation in Embolemidae. He stated: "It is therefore doubtful that their resemblance has been inherited." His argument would have benefitted from application of cladistic logic, for no such conclusion follows if one of these states is plesiomorphic. Such is in fact the case. Geniculate antennae are not characteristic of all members of any chrysidoid family, being absent in Plumariidae, Scolebythidae, Sclerogibbidae, various Bethylidae and loboscelidiine chrysidids as well as most Dryinidae. Geniculate antennae are certainly not characteristic of the dryinid groundplan, and so the two families do not differ in this character. An elongate scape (as long or longer than the head) and fixed pedicel/flagellum articulation are certainly derived; they are only approached elsewhere in Chrysidoidea in Loboscelidiinae. Dryinidae are therefore plesiomorphic in these states and Embolemidae autapomorphic, and relationship is not precluded by this.

Besides the structure of their antennae, Embolemidae are autapomorphic in the antennal prominence. The face is drawn out into a conical projection supporting the antennal sockets, and the entire head appears pyriform, with the frontoclypeal suture well separated from the antennal sockets.

Palpi. The number of segments in the palpi has traditionally been of use in the generic and specific taxonomy of several chrysidoid families (Chrysididae, Bohart and Kimsey, 1982; Bethylidae, Evans, 1964; and especially Dryinidae, Olmi, 1984). Reductions from the primitive state of 6-segmented maxillary and 4-segmented labial palpi (Brothers, 1975) range to complete absence of the labial palpi (e.g., *Myrmecopterinella,* Plumariidae). The primitive formula is retained in Scolebythidae, and had also been considered part of the plumariid groundplan (present in male *Heterogyna*; Brothers, 1974, 1975). However, Day (1984, 1985) established that *Heterogyna* is a sphecid. The groundplan formula in Plumariidae is therefore 6:3 (5:3 in the female), an autapomorphy. The formula of 6:3 is also a synapomorphy of (Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae). Further reductions characterize the groundplans of Sclerogibbidae and Chrysididae (to 5:3) and Embolemidae (4:2 in the female).

Mesosoma

Pronotum. Brothers (1975) considered a pronotal "collar," an anterior projection covering the propleura dorsally, to be plesiomorphic in the Aculeata, as that is generally the condition in other Hymenoptera. Absence of this collar, so that the propleura are dorsally exposed, he considered separately derived in Scolebythidae and plumariid females. Koenigsmann (1978) used reduction in the collar as his synapomorphy for Plumariidae and Scolebythidae. However, as realized by Brothers (1975:502), the derived state was attained by different modifications in the two groups. Male plumariids do have a relatively short collar. In plumariid females the collar is absent, and the pleura are fused both dorsally and ventrally, forming a rigid tube (Evans, 1966:fig. 11). The pronotum is enlarged relative to the rest of the thorax, a common modification in wingless chrysidoid females (Reid, 1941:figs. 42–54). In scolebythids the pleura are simply produced anteriad; no pronotal modification or pleural fusion occur. The collar is also absent in some other wingless female chrysidoids, e.g., *Pseudogonatopus.* Therefore there is little doubt that the loss of the collar is convergent, and not very similar, in the two groups.

Prosternum. Evans (1963) in his description of Scolebythidae, noted that the large prosternum was an unusual character in Hymenoptera. The propleura are widely separated posteriorly, and the sternum flat. Brothers (1975) called this the primitive extreme, but also stated "Since this condition is more extreme than in any other taxon, it may be a secondary development." This is most likely the case. Only the uniform plane of the prosternum is plesiomorphic. Thus the prothorax of scolebythids is highly modified, for in addition to the reduced pronotal collar, divergent pleura and enlarged prosternum, the coxae are also apomorphic. They are basally separated but produced posteriorly beyond the trochanteral insertions so that they are contiguous apically, a unique condition in Aculeata (Brothers, 1975).

Evans (1973) described the Cretaceous *Cretabythus* as a doubtful scolebythid. The single specimen was stated to have the prosternum "not evident," in addition to having a short pronotal collar. The fore coxae were described as contiguous, but no further details were given. The wing venation appears to be that of a scolebythid, but as the prothoracic modifications are the crucial autapomorphies of the family, it is possible that this assignment is incorrect. If the placement is upheld, it conclusively establishes the secondary nature of the prothoracic characters of extant Scolebythidae.

Depression of the prosternum is an autapomorphy of the Plumariidae (Brothers, 1975). The prosternum has only the anterior part visible, the posterior part being depressed in a different plane from the rest of the sternum. In other chrysidoids the prosternum is in a uniform plane when visible (it is very reduced in embolemids and sclerogibbids), as is also the case in ichneumonoids.

Fore legs. The apomorphic production of the coxae in scolebythids has been alluded to previously. Additional characters include the enlarged femora in sclerogibbids, and the tarsal chela of dryinids. The fore femora are larger than those of succeeding legs in both male and female sclerogibbids, but are enormously swollen in females (see fig. 2 in Krombein, 1979). This is one of the most recognizable traits of the family, and is an outstanding autapomorphy. The femora are often enlarged in females of other Chrysidoidea (Bethylidae, Embolemidae, Dryinidae) but not to the same degree nor more than succeeding legs (exception in Bocchinae). The chela formed by the fifth tarsal segment and one enlarged unguis of female dryinids is an adaptation for seizing the host prior to oviposition. Other modifications of the fore legs are associated with its development (Richards, 1939a). It is not found in females of the subfamilies Aphelopinae and Biaphelopinae, therefore it is not a groundplan feature of the Dryinidae. Rasnitsyn (1980) listed enlarged ungues of the anterior tarsi in females as a synapomorphy of Sclerogibbidae and Dryinidae, but noted that only one unguis was enlarged in only some dryinids, and so this was a "common tendency" rather than a common character. It is worth pointing out that even this is incorrect; the claws of the two families are not at all similar. The ungues of sclerogibbids are not enlarged; the arolium is. The ungues are no larger than those of any other chrysidoid, but the expanded arolium is autapomorphic. In dryinids with the chela, the arolium is elongate and the orbicula well-sclerotized and covering most of the dorsal surface. Aphelopinae and Biaphelopinae have plesiomorphic claws (Olmi, 1984).

Tibial spurs. The plesiomorphic spur formula is 1-2-2 in Aculeata (Brothers, 1975). This is the condition in most Chrysidoidea. The formula is 1-1-2 in Embolemidae + Dryinidae, one mid tibial spur having been lost. This is a synapomorphy of the two families (Koenigsmann, 1978). There has been further reduction in some Dryinidae, to no mid tibial spurs in some groups (list in Olmi, 1984).

Koenigsmann (1978) also listed the fore tibial spur as a possible autapomorphy of the Embolemidae. The calcar is short, strongly curved and has a strongly truncate apex in female embolemids. The state in other chrysidoids is generally that which Brothers (1975) considered plesiomorphic in Aculeata, namely more or less straight and with an acute apex.

Metasternum. Brothers (1975) considered a metasternum with the mesal section in approximately the same plane as the mesosternum, and the lateral thirds depressed to accommodate the mid coxae, to be primitive in Aculeata. The basis for this interpretation was "because this is the condition in various aculeates that are considered to be the most primitive on the basis of other characters." The state with the metasternum depressed anteriorly and laterally so that the mid coxae are nearly contiguous he considered apomorphic, and the state of the metasternum completely depressed further derived from this. These latter two states are only found within Plumariidae (female and male, respectively) in the Chrysidoidea.

Rasnitsyn (1980) disputed this hypothesis, but he did not characterize it completely correctly. He considered a metasternum with "its middle portion raised in the form of a clearly demarcated platform forcing the mesocoxae widely apart," as in Bethylidae, to be apomorphic. A median carina on the metasternum in Embolemidae and Chrysididae (with two carinae in Cleptinae) "may be the precursor or rudiment of the broad platform." Rasnitsyn further stated that according to Brothers a platform is present in female plumariids, which Brothers did not indicate, and that in other Chrysidoidea the metasternum is more or less flat, without a platform or carina. The platform Rasnitsyn reasoned to be apomorphic because: 1) it "probably was not developed as yet" in the Jurassic Bethylonymidae, which he treats as the ancestor of Aculeata; and 2) it is absent in Sclerogibbidae and ants, "many of which are close in their mode of preying (inside the substratum) to the forms furnished with a platform." Therefore it developed secondarily, because Rasnitsyn believed prey searching in the substrate to be primary for Aculeata.

It is probable that the anteriorly broad metasternum found in Bethylidae is in fact apomorphic. The metasternum is usually anteriorly narrow in other Chrysidoidea, primitive Sphecoidea and Ichneumonoidea. The sternum is not differentiated into approximate thirds, and is depressed anterolaterally in many ichneumonoids. It is therefore probably most parsimonious to regard an anteriorly narrow metasternum in approximately the same plane as the mesosternum as plesiomorphic for Aculeata (Brothers' state 38.1), including female Plumariidae. Then a raised (i.e., anteriorly broad) metasternum is separately derived in the Bethylidae and some Vespoidea (Brothers, 1975, state 38). Some chrysidids (Cleptinae) also have an anteriorly broad sternum, but as most do not, and a broad sternum and carinae may be found in members of other families (e.g., Dryinidae), this appears to be convergent. Embolemids and chrysidids in general are no more similar to bethylids in the metasternum than are scolebythids, sclerogibbids or dryinids. The contention that the carinae of Embolemidae and Chrysididae are homologous with the anteriorly broad sternum of bethylids is unfounded; there is no logical reason for one state to be a transformation of the other. Finally, under this interpretation, the completely depressed metasternum of male plumariids is autapomorphic, a state also found in some Vespoidea (Brothers, 1975).

Metapostnotum. Obliteration of the metapostnotal-propodeal suture and reduction of the metapostnotum to lateral remnants only was used by Brothers (1975) as a synapomorphy for Scolebythidae and his "bethylid" group. This suture is still visible in male Plumariidae. However, as pointed out by Rasnitsyn (1980), the suture is present in *Ycaploca,* a scolebythid not seen by Brothers (and also in the putative fossil scolebythid *Cretabythus*). Rasnitsyn also claimed that "the posterior boundary of the metapostnotum also persists in primitive Dryinidae (Aphelopinae and Anteoninae)." The suture is not present in any members of these subfamilies that I have examined, and Olmi (1984) makes no reference to this suture in any dryinid. Also, Olmi's figures of Aphelopinae, Biaphelopinae and Anteoninae do not show this suture. Therefore I regard Rasnitsyn's statement as an error, and treat constriction of the metapostnotum as a synapomorphy for (Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae). This state is convergently derived in some Scolebythidae.

Propodeum. Brothers (1975) pointed out that the metathoracic-propodeal suture was completely obliterated ventral to the endophragmal pit but discernible dorsally in the chrysidoids examined by him. This is an apomorphy appearing six times on his cladogram. The state also obtains in the chrysidoid families he did not see, and so is autapomorphic for the superfamily.

The propodeum has probably accounted for most of the citations of Mesitiinae as transitional to Chrysididae (Ashmead, 1902; Reid, 1941; Moczar, 1970; Koenigsmann, 1978; Rasnitsyn, 1980). In Mesitiinae, as in most chrysidids, the propodeum bears spiniform projections on the lateral angles. These projections are apomorphic, and are the most significant feature linking mesitiines to chrysidids. Other characters suggested as being similar in the two groups cannot bear interpretation as synapomorphies: The reduced venation of mesitiines (three closed cells with the marginal cell more or less open) shows the same pattern as various cleptines and amisegines, groups to which they have most often been likened (Ashmead, 1902; Moczar, 1970). However, this pattern is not the groundplan of the Chrysididae, as discussed above, nor of Amiseginae (cf. figs. in Krombein, 1957). The integument structure (Koenigsmann, 1978) is not relevant; Mesitiinae do not have metallic coloration (Nagy, 1969; it is variable in chrysidids anyway) and the punctation is no coarser in mesitiines than other bethylids such as *Pristocera* (and is also variable in chrysidids). Of the thoracic characters discussed by Reid (1941), the longitudinal furrow of the pronotum appears in numerous unrelated groups (cf. figs. in Reid, 1941), as is true of the furrows of the propodeal dorsum. A separate epicnemium with the sclerites ventrally in contact is primitive in Aculeata (Brothers, 1975). Rasnitsyn (1980) questioned this (and incorrectly referred to these sclerites as the postspiracular), but as documented in Richards (1977) this is primitive in Hymenoptera as a whole. The spiniform projections are therefore the only "transitional" feature, the other characters mentioned being either plesiomorphies, which are inconsequential, or highly variable characters of little weight. Bohart and Kimsey (1982) apparently did not consider these projections as a groundplan characteristic of Chrysididae. This might be incorrect; spiniform armature does not occur in Loboscelidiinae and various Amiseginae (Krombein, 1957), which are treated as sister-groups in Bohart and Kimsey's cladogram, but some type of projection from the lateral angles is otherwise rather general in the family. However, even if spiniform projections are a shared apomorphy of mesitiines and chrysidids, this is most parsimoniously treated as convergent in light of the characters mesitiines share with other bethylids.

Metasoma

Number of visible segments. Internation of the seventh metasomal tergum of the female is one of the outstanding autapomorphies of the Sphecoidea + Vespoidea (Aculeata s. str.) (Oeser, 1961; Brothers, 1975). Seven visible metasomal segments is the usual condition in Chrysidoidea, although the seventh may be somewhat reduced. Thus, internation of the terminal segments in both sexes and development of the telescoping ovipositor tube is a primary autapomorphy of the Chrysididae. There are four visible terga in the female and five visible in the male in the groundplan, the state found in Cleptinae and Amiseginae. Further segments are retracted in other subfamilies, and failure to appreciate that this is part of a transformation series starting with the four/five condition is perhaps partly responsible for the confusion over the definition of the Chrysididae and its constituent taxa over the past century (documented in Reid, 1941; Krombein, 1957; Day, 1979). This has only been settled recently (Day, 1979). On the cladogram of Bohart and Kimsey (1982) the series is four-three-two in females, and five-four-three-two in males. These transformations define various components of the cladogram, but it should be noted that the states are not optimally distributed in their rendition. The metasomal internation states appear multiple times unnecessarily; the four/five condition appears twice when in fact it is characteristic of the entire family, and three visible terga in the male also appears twice.

Articulation between sternum I and II. The relationship between the first and second metasomal sterna provides critical characters for Rasnitsyn's (1980) system of Aculeata. Apart from the supposed synapomorphy described previously for his Embolemidae + (Bethylidae + Chrysididae), displacement of this articulation to the second tergum is one of the important characters for his Scolioidea. Rasnitsyn is the first author to have investigated the characters associated with this articulation, but has failed to demonstrate his putative synapomorphies. The apomorphy in Chrysidoidea is a thick, straight sternum I butt-joined to II, and a straight margin to II with small lateral notches, invaginated edges and small desclerotized areas posterior to the invaginations. The plesiomorphic alternative is a thin, rounded sternum I overlapping II, and II straight but without invaginated edges, and notches if present medial. Rasnitsyn considered the Chrysididae to be further derived, with a thin margin to I consisting of membranous lobules overlapping II, and II with the desclerotized areas expanded onto the anterior margin so that it is deeply notched, with the invaginations reduced but the rudiments discernible in Adelphinae (=Amiseginae). Actually this calls into question the homology. The interpretation can only be upheld on the basis of other characters, for it is not due to any intrinsic similarity. As discussed elsewhere in this paper, none of the other characters adduced by Rasnitsyn for grouping embolemids with Bethylidae + Chrysididae are acceptable synapomorphies, and they conflict with characters establishing the cladogram of Figure 4. Further, there does not appear to be any special similarity between Embolemidae and Bethylidae. Embolemids in fact have sternum I as thin as succeeding sterna, and it actually overlaps sternum II much as in other Chrysidoidea (cf. especially the nearctic *Ampulicomorpha,* not discussed by Rasnitsyn, with Scolebythidae and Plumariidae). The resemblance between embolemids and bethylids is no more pronounced than that between chrysidids and those dryinids with a lobate sternum I (various gonatopodines in addition to Aphelopinae mentioned by Rasnitsyn). These characters do not appear to be useful in associating taxa. It may be added that this is also the case where Rasnitsyn discusses the sterna in Scolioidea; the supposed autapomorphy does not characterize all of the Scolioidea, and is found in other groups (vespids and formicids).

Sting. The terminology employed here is primarily that of Snodgrass (1933), used by Oeser (1961), Richards (1977), Evans et al. (1979) and Rasnitsyn (1980). The terminology of Smith (1970) is also given, as that was employed by Brothers (1975).

Articulation within second valvifer. The presence of a postincision (incisura postarticularis of Oeser), a dorsoventral constriction within the second valvifer (section 1 of gonocoxite IX) is one of the primary autapomorphies of the ovipositor of the Aculeata (Oeser, 1961; Brothers, 1975; Koenigsmann, 1978; Rasnitsyn, 1980). It divides the valvifer into dorsal and ventral arms (oblong plate and lamina falcata). Other Hymenoptera lack this, and along with other characters of the female terminalia such as loss of cerci and tergum VIII apophyses, this firmly establishes the monophyly of the Aculeata. Chrysidoidea are further apomorphic in having this constriction divided by an articulation (Figs. 17, 22, 23). This is universal in the group (Oeser, 1961; Brothers, 1975; Rasnitsyn, 1980), including Plumariidae (Brothers, 1974, 1975 and verified by dissection of a female in the collection of the U.S. National Museum), and is thus a perfectly consistent autapomorphy.

Furcula. Oeser (1961) treated presence of a furcula (Figs. 17, 18, 23), the detached basal part of the second valvulae (notum of gonapophyses IX), as an autapomorphy of the Aculeata. This interpretation was followed by subsequent authors until Rasnitsyn (1980). Observing that the furcula is absent in Sclerogibbidae, Embolemidae and Dryinidae (Fig. 22), as well as some ants, Rasnitsyn suggested that development of this sclerite may have been a tendency in Aculeata rather than a character of the common ancestor. The sclerite is of diverse form in aculeates (figs. in Hermann and Chao, 1983). Typically it is tripartite, with ventral arms articulating with the second valvulae (Fig. 18), but it may be differently shaped, and certainly has been lost in Formicidae (cf. Hermann and Chao, 1983). However, it is most parsimonious to regard the structure as present in the groundplan of aculeates. Oeser (1961:fig. 41) illustrated a structurally simple "furculaähnliche" sclerite at the base of the second valvulae in some ichneumonoids and evanioids, and Hermann and Morrison (1979) described a furcula in the ovipositor of a braconid. The latter authors concluded that the furcula arose prior to the origin of aculeates, for otherwise it "has had a polyphyletic origin." Ichneumonoidea should be further investigated with respect to the structure of their supposed furcula. They are the sister-group of Aculeata (Mason, 1986b), and if a furcula is indeed widespread in the group, it must be inferred to have been present in the common ancestor of the Aculeata—where it was a primitive trait. Even if it should turn out that a furcula is a convergent development in some ichneumonoids, considering the generality of this sclerite in aculeates, it is still parsimonious to treat it as an ancestral aculeate character.

Following this interpretation, absence of a furcula is therefore a synapomorphy for the sclerogibbids, embolemids and dryinids. This is supported by the similar basal elongation of the second valvulae into a process in the three families (Figs. 19–22; cf. Rasnitsyn, 1980:figs. 147b, e, f). Rasnitsyn noted the similarity of embolemids and dryinids in this character, but argued that in Embolemidae the process was compressed into a "vertical lamella resembling the unpaired part of the furcula in Bethylidae." However, elsewhere he cited the formation as a synapomorphy of dryinids and sclerogibbids, "even though the process thus formed differs in shape in the two groups." Based upon my own dissections, the differences between dryinids and sclerogibbids are no greater than those between these families and embolemids. The supposed similarity of embolemids to bethylids is *ad hoc*; it is only a necessary inference given Rasnitsyn's grouping of embolemids, bethylids and chrysidids. Dryinids and sclerogibbids are no less similar to bethylids, but more important, are essentially the same as embolemids. A synapomorphy for Sclerogibbidae + (Embolemidae + Dryinidae) is the best conclusion with regard to the absence of the furcula.

Articulation between second valvulae and valvifer. The second valvifers (gonocoxites IX) articulate with the second valvulae (gonapophyses IX; sting) via a pair of articular processes at the base of the valvulae (Figs. 17, 22) in most Hymenoptera including Aculeata. As noted by Oeser (1961), Bethylidae and Chrysididae lack a functional articulation. The proximal arm of the second valvifer is well separated from the base of the valve (Fig. 23; Oeser, 1961:figs. 47, 102; Rasnitsyn, 1980:figs. 147c, d). This is synapomorphic for the two families, as Rasnitsyn (1980) realized. Both groups possess further modifications. Chrysididae have most parts of the sting reduced, and function is lost in some groups. Some Bethylidae have a secondary articulation between the distal arm of the second valvifer and second valvulae via elongate processes from the valvifer (*Cephalonomia,* Oeser, 1961; *Bethylus,* Rasnitsyn, 1980). These further apomorphies are not general (*Pristocera,* Fig. 23, and *Pilomesitius* lack the secondary articulation; and the sting of most chrysidids has not been described in much detail).

Life history

Hosts and habitats. Rasnitsyn (1980) believed prey searching within the substrate ("probably of beetle larvae in decayed wood") to be the primitive condition in Aculeata, and indeed, it is widespread in diverse groups. In Chrysidoidea, most bethylids do attack beetle larvae (e.g., list in Evans, 1978), and the hosts of *Ycaploca*

(Scolebythidae) are probably wood-boring cerambycids (Brothers, 1981). Other scolebythids have been collected in wood (Evans et al., 1979), and plumariid females are hypogaeic (Evans, 1966). Chrysidids have diverse hosts, but these are attacked at stages where they are leading a "confined existence" (Rasnitsyn, 1980). The hosts range from tenthredinoid larvae (Cleptinae) to phasmid egg cases (Amiseginae + Loboscelidiinae) to aculeate larvae (most members of the remaining subfamilies). Sclerogibbidae attack Embiidina, certainly an autapomorphy. Embolemidae have been reared from nymphs of a fulgoroid living in rotting wood (Bridwell, 1958). Finally, Dryinidae attack a variety of Homoptera Auchenorrhyncha, mostly free-living Fulgoroidea and Cicadellidae (see list in Olmi, 1984).

The shared host taxon of embolemids and dryinids is here considered a synapomorphy. Rasnitsyn (1980) denied this interpretation. He considered embolemids' "similarity to Bethylidae and Chrysididae with regard to the habitat of their hosts" to be "as important as the taxonomic closeness of the hosts of Embolemidae and Dryinidae." Further, he treated active, non-Holometabola hosts as a synapomorphy between Dryinidae and Sclerogibbidae. These tenuous homologies are quite incredible; by Rasnitsyn's own interpretation the host habitat shared by Embolemidae, Bethylidae and Chrysididae is plesiomorphic. The embiid nymphs attacked by Sclerogibbidae are no more free-living than the achilid nymphs attacked by Embolemidae. And non-Holometabola is scarcely acceptable as a synapomorphic host group if Homoptera Auchenorrhyncha is not.

Endoparasitism. Most Dryinidae share a highly distinctive life history (summary in Olmi, 1984). The first larval instar is endoparasitic, but later instars protrude from the host as a cyst formed by cast exuviae. In Aphelopinae, at least the first instar is surrounded by a hypertrophied mass of host tissue, the trophamnion (Olmi, 1984). This persists until the final larval instar, but the second instar protrudes through this to form the cyst of exuviae, although it is of different texture from that of other dryinids (Olmi, 1984). This cyst is certainly apomorphic, and embolemids have a similar state. Bridwell (1958) described a "translucent, rounded mass" protruding from the host of *Ampulicomorpha confusa,* and R. A. Wharton (*in litt.*) also observed a protruding sac while rearing this species. The origin of the sac was not determined in these cases, and may have been formed by host tissue. This is little different from Aphelopinae, and both families are further similar in pupation in a cocoon formed away from the host.

Rasnitsyn (1980) characterized the life history of Embolemidae as "completely endoparasitic," and stated that this "finds its analogy among Aculeata only in Chrysididae, but not in Dryinidae." Although Bridwell's wording is somewhat ambiguous, this author stated that the biology of *A. confusa* "is in all essential particulars a dryinid biology," and this is also concluded by R. A. Wharton (*in litt.*). Rasnitsyn's statements contain another error. The reference to an endoparasitic chrysidid is apparently to *Chrysis neglecta* (Maneval, 1932; now placed in *Spinolia*), but this species is reported to be external during the first instar. A more "completely endoparasitic" development is found in a dryinid, *Aphelopus* (now *Crovettia*; Olmi, 1984) *theliae,* a polyembryonic parasitoid without any external sac. Embolemids and dryinids have the same basic life history, which is a synapomorphy.

DISCUSSION

Most of the groups of the cladogram resulting from this study (Fig. 4) are supported by more than one character, as shown in the section on groundplan diagnoses. The features discussed are generally consistent, even the characters of the wing venation. The only component apparently problematic is (Sclerogibbidae + (Embolemidae + Dryinidae)) + (Bethylidae + Chrysididae). The only problematic term is Dryinidae. Both groups are supported only by homoplasious characters, which show convergent development in other groups. The arrangements suggested here based on the homoplasious characters are most parsimonious when all characters are considered. For the characters of the component, reduction of the labial palpi has also occurred in Plumariidae, and constriction of the metapostnotum within Scolebythidae. Plumariids are excluded from the component by the venational characters uniting Scolebythidae with the remaining five families, as well as their plesiomorphic metapostnotum. Scolebythids are excluded by the palpal character, and an unconstricted metapostnotum is found in *Ycaploca.* Only one autapomorphy has been identified for Dryinidae, and reduction of the fore wing venation to five closed cells occurs in several other groups. However, as discussed above, it is not part of the groundplan of these latter groups. The remaining components and terms are all supported by unique features. Therefore this cladogram may be regarded as quite strong overall.

Of the relationships established here, that between Plumariidae, Scolebythidae and the component formed by the remaining families is the same as that suggested by Brothers (1975:fig. 2) for Plumariidae, Scolebythidae and his "bethylid group," despite some changes in character state interpretations. Brothers' final cladogram (Fig. 1) was different, but he did not see all the taxa nor was this based on analysis. Koenigsmann (1978) grouped Embolemidae and Dryinidae, the traditional concept strongly corroborated here, but his other suggested relationships (Fig. 2) are rejected in this study. Koenigsmann considered all the chrysidoid families, but drew his data from a literature survey and did not attempt a comprehensive treatment of all the characters he mentioned. Partly as a result, several of his character interpretations are unacceptable. Sclerogibbidae were removed from Aculeata based on presumed primitive antennae, but as shown in this paper this must be considered a reversal. As for his suggested relationship of Plumariidae + Scolebythidae based on loss of the pronotal collar, as Brothers mentioned and as is discussed above, the states in these two families are actually different.

The relationship established between Sclerogibbidae and Embolemidae + Dryinidae was previously unsuspected, but that between the latter two families, and Bethylidae + Chrysididae are inveterate views. Rasnitsyn (1980) accepted the last group, but otherwise proposed a very different system (Fig. 3). As discussed in the preceding section, his system is unsupportable even on the basis of the characters used in establishing it. Although using cladistic terms, he frequently grouped by symplesiomorphy, or trends not groundplan characters. Several of his synapomorphies are dubious homologies, or do not characterize all members of the groups based on them. This is partly due to his rejection of cladistic methods; he was thus unable to properly evaluate the informativeness of his characters. And partly it is due to his use of fossil taxa as recognized ancestors in ancestor-descendant relationships, a fallacious procedure (Hennig, 1966; Engelmann and Wiley, 1977). For Aculeata, Rasnitsyn considers the Jurassic Bethylonymidae as the ancestor, even though it had an external ovipositor and multisegmented antennae (that is, possessed none of the aculeate autapomorphies). In his discussion of the metasternum, although he apparently could not see the metasternum on his specimens of this taxon, he stated that a metasternal "platform" was "probably not developed as yet" and thus is a derived feature in extant taxa. This is one of the crucial characters of his system, and many of his *ad hoc* interpretations of other characters are necessary to conform to it. Although his work presented new data, in general it must be reanalyzed before it is of any use in phylogenetic inference. Where I have done so his interpretations are not upheld.

In conclusion, it is worth emphasizing that one of the reasons cladistics has had great impact on systematics is that there is a strong relationship between evidence and hypothesis. Groups can only be recognized on the basis of characters, not general resemblance. This study has built on previous work, but has been more comprehensive in that more evidence has been adduced and analyzed. The result (Fig. 4) is correspondingly better able to account for the available evidence, and so is the best present hypothesis of the phylogenetic relationships of the Chrysidoidea.

ACKNOWLEDGMENTS

This research is based primarily on the Chrysidoidea collection of the U.S. National Museum, and was supported by a Smithsonian Postdoctoral Fellowship to the author. I would like to thank K. V. Krombein and A. S. Menke of the U.S.N.M. for making the collection and resources of the Smithsonian available to me, and the Ashmead Club for moral support. M. D. Bowers and S. R. Shaw, Museum of Comparative Zoology, and M. E. Schauff, U.S.N.M., read early drafts of this paper, and H. E. Evans, Colorado State University, discussed the conclusions with me. This work has benefitted from their criticism. I would especially like to thank K. V. Krombein; A. S. Menke; M. C. Day, British Museum; W. R. M. Mason, Canadian National Collection; L. S. Kimsey, University of California; and D. J. Brothers, University of Natal, for critical suggestions on a later draft, many of which I adopted. M. J. Sharkey of the Canadian National Collection made a translation of Rasnitsyn's work available to me.

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LIST OF TAXA EXAMINED

The taxa examined were selected to maximize diversity of higher categories represented. In the four smaller chrysidoid families all available species were studied, whereas for the three larger families emphasis was at the generic level. Survey of outgroups was by exemplar taxa, with particular attention to Ichneumonoidea (Doryctinae, Helconinae and Pimplinae) and Sphecidae (Sphecinae). The specimens are deposited in the collections of the U.S. National Museum and the Museum of Comparative Zoology.

PLUMARIIDAE
Plumarius sp. (female and male)
Plumaroides andalgalensis
Myrmecopterinella okahandja

SCOLEBYTHIDAE
Clystopsenella longiventris
Scolebythus madecassus
Ycaploca evansi

SCLEROGIBBIDAE
Probethylus callani
mexicanus

  schwarzi
  sp.
Sclerogibba citipes
  magrettii ?
  taprobanana
  spp.

EMBOLEMIDAE
Ampulicomorpha confusa
  sp.
Embolemus nearcticus
  ruddii
  spp.

DRYINIDAE
  APHELOPINAE
Aphelopus albopictus
  bicolor
  diffusus
  maculiceps
  melaleucus
  nigriceps
  orientalis
  rufiventris
  varicornis
Crovettia theliae
  sp.

  ANTEONINAE
Anteon ephippiger
  flavicorne
  gaullei
  jurineanum
  puncticeps
  scapulare
  spp.
Deinodryinus asiaticus
  atriventris
  spp.
Lonchodryinus ruficornis
  sp.

  BOCCHINAE
Bocchus flavicollis
  mirabilis
  richardsi
  robustus
  rubricus
Mirodryinus xerophilus

  THAUMATODRYININAE
Thaumatodryinus sp.

  GONATOPODINAE
Acrodontochelys americanus
Apterodryinus citrinus
  secundus
Dicondylus perkinsi
Echthrodelphax hortusensis
Esagonatopus niger
Gonatopus breviforceps
  daunus
  ombrodes
  subtilis
Haplogonatopus apicalis
  hernandezae
Neodryinus koebelei
  trinitatis
Neogonatopus fentoni
Pseudogonatopus albosignatus
  hospes
  ortholabis
  sarawaki
  sjoestedti
  spp.
Tetrodontochelys anomalus
  obscurus
  plesius
  unicus
Trichogonatopus albomarginatus

  DRYININAE
Dryinus alatus
  antilleanus
  browni
  lankanus
  pulcher
  stantoni
  surinamensis
Richardsidryinus erraticus
Trydryinus gibbosus
  poecilopterae
  ruficauda
  ruficeps

BETHYLIDAE
  MESITIINAE
Anaylax aegyptius
Clytrovorus horvathi
Codorcas cursor
Mesitius apterus
  ghilianii

spathulifer
sp.
Metrionotus egypticus
Pilomesitius madagascarensis
Sulcomesitius africanus
brevidens
consimilis
krombeinii
rieki
szentivanyi
vechti
vietnamensis

PRISTOCERINAE

Apenesia amazonica
malaitensis
Dicrogenium sp.
Dissomphalus punctatus
xanthopus
Neodicrogenium sp.
Parascleroderma nigrum
Pristocera armifera
depressus
japonica
Prosapenesia lacteipennis
Pseudisobranchium albipes
pallidipes
subcyaneum

EPYRINAE

EPYRINI

Acanthepyris sp.
Allepyris sp.
Anisepyris aurichalceus
tlaloc
Bakeriella flavicornis
inca
Calyoza sp.
Calyozina mexicana
Epyris amabilis
dodecatomus
extraneus
niger
rufipes
Holepyris crenulatus
remotus
sylvanidus
Laelius centratus
Pristobethylus sp.
Rhabdepyris apache
gracilis
luteipennis
platycephalus
viridissimus

CEPHALONOMIINI

Cephalonomia conophthori
formiciformis
Israelius carthami
Plastanoxus chittendenii

SCLERODERMINI

Chilepyris herbsti
Glenosema crandalli
silvicola
Nesepyris virginianus
Nothepyris brasiliensis
Sclerodermus cereicollis
macrogaster
sp.
Thlastepyris pertenuis

BETHYLINAE

BETHYLINI

Bethylus amoenus
arcuatus
decipiens
fuscicornis

SIEROLINI

Eupsenella agilis
sp.
Goniozus aethiops
carborum
silvestris
spilogaster
Lytopsenella herbsti
Prosierola lata
variegata
Sierola koa

CHRYSIDIDAE

CLEPTINAE

Cleptes afer
alienus
consimilis
moczari
nitidulus
rufifemur
scutellaris
semiauratus
speciosus

Cleptidia aurora
  mutilloides

LOBOSCELIDIINAE

Loboscelidia bakeri
  cervix
  collaris
  dejecta
  nigra
  philippinensis
  reducta
  rufa
  scutellata

AMISEGINAE

Adelphe anisomorphae
  mexicana
Amisega cooperi
Mesitiopterus evansi
  floridensis
  kahlii
  townsendi
Microsega bella
Myrmecosega bispinosa
Myrmecomimesis nigricans
Nesogyne taino

PARNOPINAE

Parnopes chrysoprasinus
  concinnus
  denticulatus
  edwardsii
  fischeri
  fulvicornis
  grandior

ELAMPINAE

Elampus gayi
  viridicyaneus
Hedychrydium dimidiatum
  fletcheri
  roseum
Hedychrum nobilis
Holypyga fervida
  gloriosa
  ventralis
Omalus aeneus
  auratus
  telfordi
  variatus

ALLOCOELIINAE

Allocoelia capensis

CHRYSIDINAE

CHRYSIDINI

Argochrysis mesillae
Ceratochrysis cyanosoma
  enhuycki
  kansensis
  perpulchra
  quadrituberculata
Chrysis astralia
  antennalis
  coerulans
  fuscipennis
  gibba
  ignita
  intricata
  japonica
  megacephala
  nitidula
  smaragdula
  splendens
  viridula
Chrysura austriaca
  cobaltina
  cuprea
  inusitata
  pustulosa
Chrysurissa densa
Pyria lyncea
  oculata
  stilboides
Trichrysis cyanea
  doriae
  lusca
  tridens

EUCHROEINI

Euchroeus purpuratus
Ipsiura neolateralis
Neochrysis bruchi
  carina
  panamensis
Pseudospinolia neglecta
  tetrini
Stilbum cyanurum
  splendidum
  viride

Received June 20, 1985; accepted December 16, 1985.

J. New York Entomol. Soc. 94(3):331–341, 1986

SUPPLEMENTARY STUDIES ON ANT LARVAE: FORMICINAE (HYMENOPTERA: FORMICIDAE)

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Abstract.—This article describes the five species of formicine larvae that have accumulated since the publication of our 1982 supplement to our 1976 monograph. The genus *Aphomomyrmex* has not been described previously; the other genera are *Paratrechina* and *Dendromyrmex.* Also included are references to formicine larvae in the literature.

In this article we describe five species of formicine larvae that have accumulated since the publication of our 1982 supplement to our 1976 memoir. Here we give descriptions only. In a future supplement to our 1976 memoir we will prepare keys for the separation of the various taxa.

We have noted recently in the literature a developing problem: the students of caste determination in ants need to be able to distinguish the larval instars. In the past we have rarely secured more than one instar in a sample, but now entomologists are sending us all available sizes of larvae, e.g., *Aphomomyrmex* below.

We also include any references to ant larvae of the subfamily Formicinae which we have found since our 1982 publication.

Tribe Formicini
Genus CATAGLYPHIS Foerster
Cataglyphis cursor (Fonscolombe)

Cagniant, 1980: 3 instars, each described and sketched. Duration of stages given.

Tribe Oecophyllini
Genus OECOPHYLLA F. Smith
Oecophylla longinoda (Latreille)

Hölldobler and Wilson, 1983: SEM's of labium showing opening of silk-glands.

Oecophylla smaragdina (Fabricius)

Hinton, 1951:163. The limpet-like caterpillars of *Liphyra brassolis* Westwood [Lepidoptera: Lycaenidae] feed upon the larvae of this ant: "the caterpillar lowers the edge of its carapace-like upper surface, and the ant larva is then consumed beneath the body. The caterpillars suck their juice out but do not chew them."

Hölldobler and Wilson, 1983: Colored photograph of worker using a larva as a shuttle to spin silk for the nest.

Tribe Brachymyrmecini
Genus APHOMOMYRMEX Emery

Profile pheidoloid but with narrowly rounded posterior end. Praesaepium lacking. Body hairs sparse. Of 2 types: (1) unbranched, smooth, with long flexuous tip; (2) short, unbranched, smooth with frayed tip. Labrum deeply bilobed; without chiloscleres. Mandible camponotoid but with the apical tooth long, slender and heavily sclerotized.

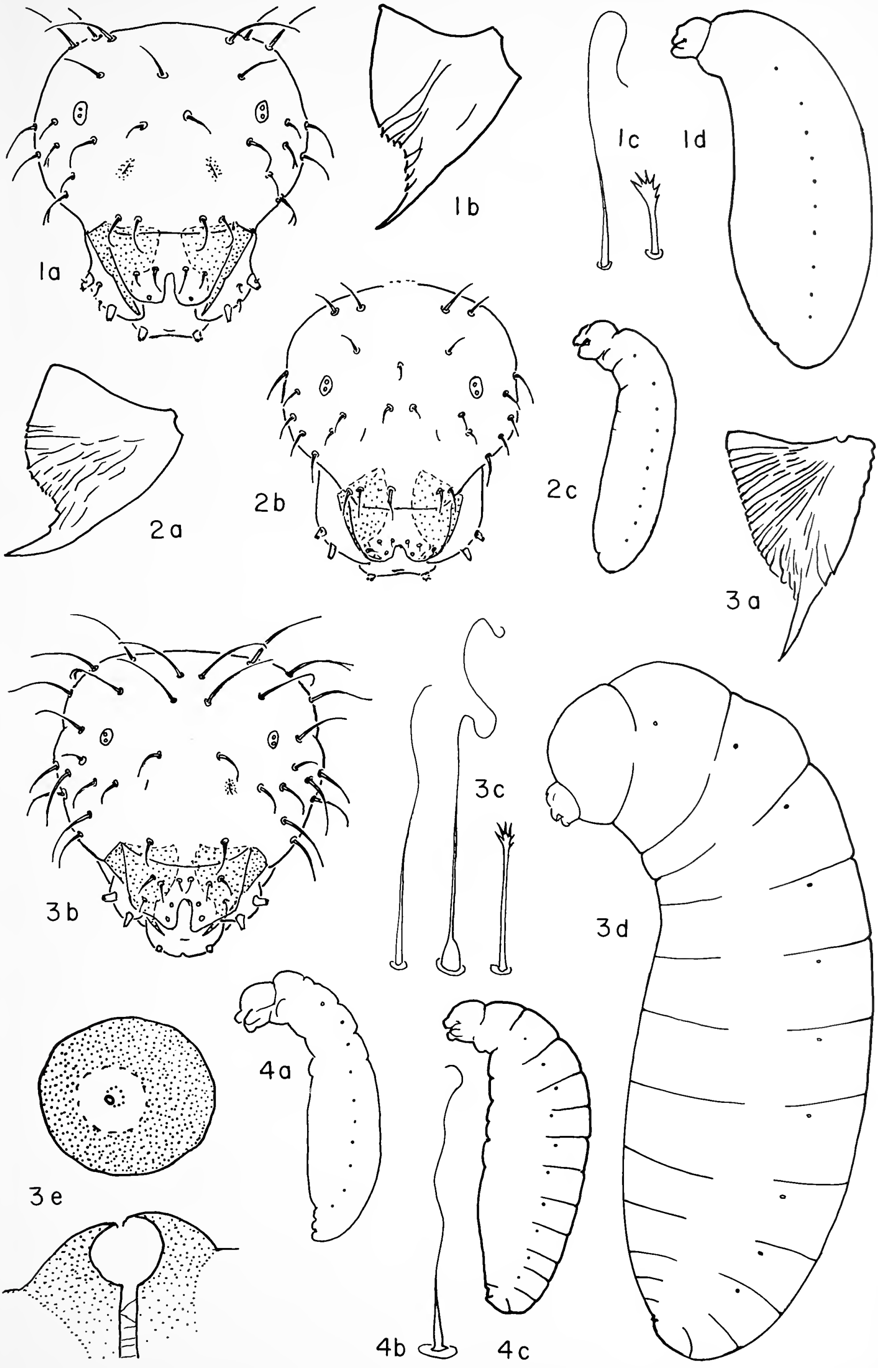
Aphomomyrmex afer Emery
Figs. 1–4

Description. MATURE WORKER LARVA. Length (through spiracles) about 2.6 mm. Profile pheidoloid but with narrowly rounded posterior end. Anus ventral. Spiracles small, decreasing slightly in diameter posteriorly. Body hairs sparse, uniformly distributed. Of 2 types: (1) 0.019–0.063 mm long, unbranched, smooth, with a long flexuous tip, on all somites; (2) about 0.025 mm long, few, with frayed tip, on AVIII–AX. Cranium transversely subelliptical, slightly wider than long. Antennae above midlength of cranium, each with 2 small sensilla. Head hairs few (about 30); 0.05–0.1 mm long, unbranched, smooth, widely scattered. Labrum large, nearly twice as broad as long, narrowed ventrally, deeply bilobed; anterior surface of each lobe with 2 or 3 short hairs and 1 or 2 sensilla; ventral surface spinulose, the spinules minute and in short rows; posterior surface densely spinulose, the spinules minute and in numerous rows radiating from dorsolateral angles and with 4–6 sensilla ventrally. Mandible large; camponotoid but with long slender heavily sclerotized apical tooth; anterior and posterior surfaces with a few longitudinal ridges which terminate on medial border in small projections making medial border erose. Maxilla with apex paraboloidal and with a few minute spinules in arcuate rows; palp a short peg with 5 (4 apical and 1 lateral) sensilla; galea digitiform with 2 apical sensilla. Labium with arcuate rows of minute spinules; palp a short peg with 5 (1 with a large capsule) apical sensilla; an isolated sensillum between each palp and the opening of the sericteries, the latter a short transverse slit. Hypopharynx spinulose, the spinules minute and in numerous short transverse rows.

YOUNG WORKER LARVA. Length (through spiracles) about 2 mm. Thorax curved ventrally, abdomen straight and with a round-pointed posterior end; diameter nearly uniform throughout. Body hairs sparse; 0.024–0.125 mm long, unbranched, smooth, very slender and flexuous, a few on each somite. Head large; cranium subhexagonal, about as broad as long. Antennae small. Head hairs 0.038–0.075 mm

⟶

Figs. 1–4. *Aphomomyrmex afer.* 1. Mature worker larva. a, Head in anterior view, ×132; b, left mandible in anterior view, ×278; c, body hairs, ×400; d, larva in side view, ×22. 2. Young worker larva. a, Left mandible in anterior view, ×278; b, head in anterior view, ×132; c, larva in side view, ×22. 3. Mature sexual larva. a, Left mandible in anterior view, ×278; b, head in anterior view, ×132; c, body hairs, ×400; d, larva in side view, ×22; e, spiracle in surface view (upper) and in optical section (lower), ×834. 4. Young larvae. a, Very young sexual larva, ×22; b, type 2 body hair, ×400; c, young sexual larva, ×22.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1b
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long. Mandible with more numerous ridges. Otherwise similar to mature worker larva.

MATURE SEXUAL LARVA. Length (through spiracles) 5.2–5.6 mm. Pogonomyrmecoid but with short stout ventrally curved neck; posterior end rounded. Anus ventral. Spiracles small, nearly uniform in diameter, each opening on a low sclerotized boss. All somites feebly differentiated. Body hairs very sparse. Of 3 types: (1) 0.063–0.139 mm long, on T1–T3 and on dorsum of AI–AIV, unbranched, smooth, flexuous; (2) 0.03–0.168 mm long, with bulbous base and long slender flexuous shaft, a few on venter of AI, increasing in number to AVIII; (3) 0.038–0.075 mm long, stout and with a straight shaft and frayed tip, on AVIII–AX; AX has only type 3. Head small; cranium subhexagonal. Antenna with 2 sensilla, above midlength of cranium. Head hairs moderately numerous (about 40), 0.025–0.125 mm long, unbranched, smooth, slightly curved, a few with bifid tips. Labrum large, deeply bilobed; anterior surface of each lobe with 4–5 short hairs and 2 isolated sensilla; with minute spinules in rows on both sides of notch; posterior surface densely spinulose, the spinules minute and in numerous rows radiating from the dorsolateral angles and with 6 sensilla ventrally. Mandible large; camponotoid but with a long sharp-pointed heavily sclerotized apical tooth; anterior and posterior surfaces with numerous longitudinal ridges. Maxillary apex paraboloidal and with spinules in short arcuate rows; palp paxilliform with 5 [2 apical, 2 lateral (1 with a large cap) and 1 basal] sensilla; galea digitiform with 2 apical sensilla. Labium small, with short rows of minute spinules; palp a short peg with 5 [4 apical (1 with a large cap) and 1 basal] sensilla; an isolated sensillum between each palp and the opening of the sericteries, the latter a transverse slit. Hypopharynx spinulose, the spinules minute and in numerous short transverse subparallel rows.

YOUNG SEXUAL LARVA. Length (through spiracles) about 2.4 mm. Anterior end curved ventrally, remainder of body straight; diameter greatest at AII and AIII, diminishing toward either end. Somites feebly differentiated. Integument spinulose, the spinules larger and more numerous posteriorly. Body hairs (1) 0.06–0.138 mm; (2) 0.05–0.075 mm; (3) 0.025–0.075 mm. Head large. Otherwise similar to mature sexual larva.

VERY YOUNG SEXUAL LARVA. Length (through spiracles) about 2 mm. Slender; thorax curved ventrally, remainder of body straight; posterior end narrowly rounded. Integument spinulose. Type 2 body hairs with the base stout but not bulbous. Head large. Apical tooth of mandible somewhat shorter and stouter and slightly curved medially. Otherwise similar to mature sexual larva.

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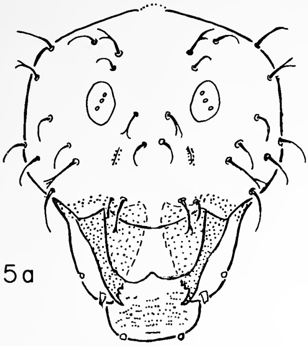
Figs. 5–7. *Paratrechina.* 5. *P. guatemalensis.* a, Head of mature larva in anterior view, ×143; b, left mandible in anterior view, ×400; c, left mandible in medial view, ×400; d, mature larva in side view, ×42; e, young larva in side view, ×42; f, head of young larva in anterior view, ×143. 6. *P. longicornis.* a, Head of young larva in anterior view, ×143; b, young larva in side view, ×42; c, left mandible of mature larva in lateral view, ×400; d, left mandible of mature larva in anterior view, ×400. 7. *P. wojciki.* a, Head of young larva in anterior view (many hairs broken off), ×143; b, left maxilla of mature larva in anterior view, ×400.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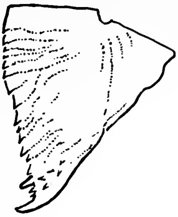
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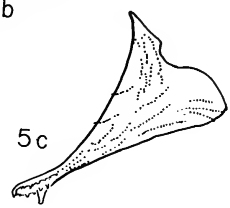
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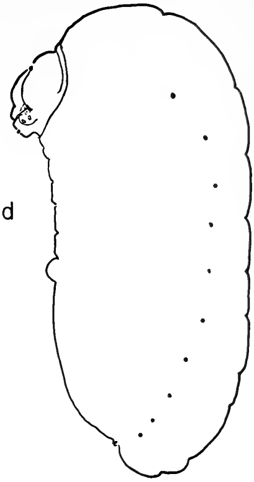
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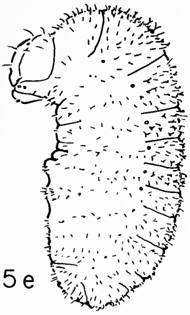
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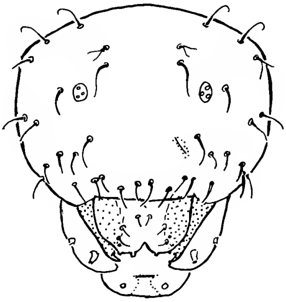
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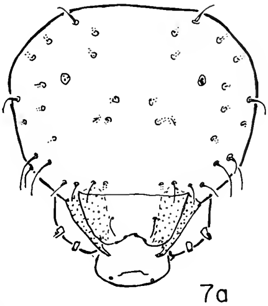
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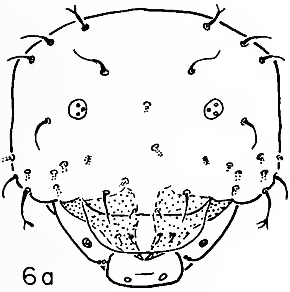
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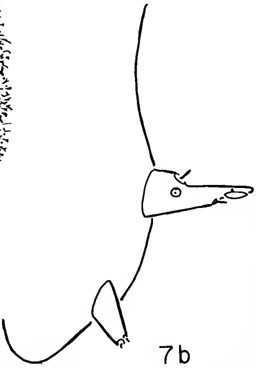
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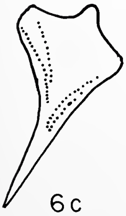
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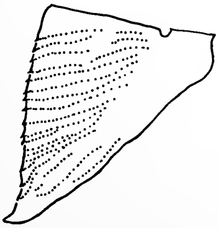

6d

Material studied. 9 larvae from Cameroon—"The Rock," Korup Forest Reserve, Ndain Dist., 8-II-1979, coll. D. McKey, courtesy of R. R. Snelling.

Genus PARATRECHINA Motschoulsky

Paratrechina guatemalensis (Forel)

Fig. 5

Description. MATURE LARVA. Length (through spiracles) about 1.8 mm. Profile dolichoderoid (i.e., short, stout, plump, straight, with both ends broadly rounded; anterior end formed from the enlarged dorsum of prothorax; head ventral, near anterior end; no neck; somites indistinct), with a small boss on venter of AIII. Anus posteroventral. Leg vestiges present. Body hairs moderately numerous, uniformly distributed, short (0.019–0.1 mm long); 2- or 3-branched. Head large; cranium subheptagonal in anterior view, breadth 1.4 times length. Antennae just above midlength of cranium, large and with 3 sensilla, each bearing a spinule. Head hairs few (about 36), short. Of 2 types: (1) 0.038–0.06 mm long, unbranched, smooth; (2) about 0.038 mm long, with bifid tip. Labrum bilobed, breadth 1.7 times length; anterior surface of each lobe with 2 minute hairs and numerous closely spaced rows of minute spinules ventrolaterally; ventral surface of each lobe with 2 or 3 isolated sensilla; entire posterior surface spinulose, the spinules minute and in rows radiating from the dorsolateral angles and with 6 isolated sensilla. Mandible moderate-sized; teeth heavily sclerotized; moderately stout, camponotoid (i.e., subtriangular, base broad, apex forming a round-pointed tooth, with 1 subapical tooth); medial surface of apex with 2 rows of denticles one anterior and the other posterior, with the subapical tooth projecting anteriorly; anterior and posterior surfaces with numerous rows of minute spinules. Maxilla appearing adnate; palp paxilliform with 5 (1 with a large capsule) sensilla; galea digitiform with 2 apical sensilla. Labium with numerous arcuate rows of minute spinules; palp a low knob with 5 sensilla; an isolated sensillum between each palp and the opening of the sericteries, the latter a short transverse slit. Hypopharynx spinulose, the spinules minute and in rows radiating from the dorsolateral angles.

YOUNG LARVA. Length (through spiracles) about 1.2 mm. Profile pheidoloid, but anterior end formed from dorsum of T1 and T2. Anus with small anterior and posterior lips. Somites feebly differentiated. Integument spinulose on venter of anterior somites and all surfaces of posterior somites. Body hairs shorter (0.025–0.063 mm long). Antenna medium-sized. Head hairs shorter, all 0.025–0.05 mm long. Galea digitiform. Otherwise as in the mature larva.

Material studied. 5 larvae from Florida—Homestead Air Force Base, Dade Co., 29-XII-1975, coll. G. C. & J. Wheeler.

Paratrechina longicornis (Latreille)

Fig. 6

Description. MATURE LARVA. Length (through spiracles) 1.8–2.1 mm. Profile dolichoderoid, without ventral boss. Body hairs shorter (0.025–0.075 mm long). Head hairs slightly shorter (0.025–0.05 mm long). Labrum without spinules on anterior surface. Mandible camponotoid, without subapical tooth; lateral view of apex thin and blade-like. Maxillary palp a slight elevation with 5 sensilla; galea represented by 2 contiguous sensilla. Labial palp represented by a cluster of 5 sensilla. Otherwise similar to *P. guatemalensis.*

YOUNG LARVA. Length (through spiracles) about 1.3 mm. Body profile more slender and lacking ventral boss. Galea represented by 2 contiguous sensilla. Otherwise similar to young *P. guatemalensis.*

Material studied. 5 larvae from Florida—Homestead Air Force Base, Dade Co., 29-XII-1975, coll. G. C. & J. Wheeler.

Paratrechina wojciki Trager

Description. MATURE LARVA. Length (through spiracles) about 1.5 mm. Integument of venter of anterior somites with minute spinules. Body hairs (1) 0.013–0.03 mm long, unbranched, smooth, on all somites; (2) 0.019–0.03 mm long, 2-branched (rarely 3-branched), on all somites. Head hairs all unbranched and smooth, 0.024–0.044 mm long. Maxillary palp a tall cone with 2 tall apical sensilla, 1 subapical with a spinule and 2 lateral sensilla with a spinule each; palp a short cone with 2 apical sensilla. Otherwise similar to *P. guatemalensis.*

YOUNG LARVA. Length (through spiracles) about 0.77 mm. Body hairs of 2 types: (1) 0.006–0.036 mm long, unbranched, smooth; (2) 0.012—0.048 mm long, 2-branched, on all somites. Head hairs of 1 type; 0.024–0.036 mm long, unbranched, smooth. Maxillary palp a slender tall cone with 2 tall apical sensilla, 1 subapical with a spinule and 2 lateral with a spinule each; palp shorter, with 2 apical sensilla. Otherwise as in young larva of *P. guatemalensis.*

Material studied. 5 larvae from Florida—Pinelands Trail, Everglades National Park, 30-XII-1975, coll. G. C. & J. Wheeler.

Tribe Camponotini

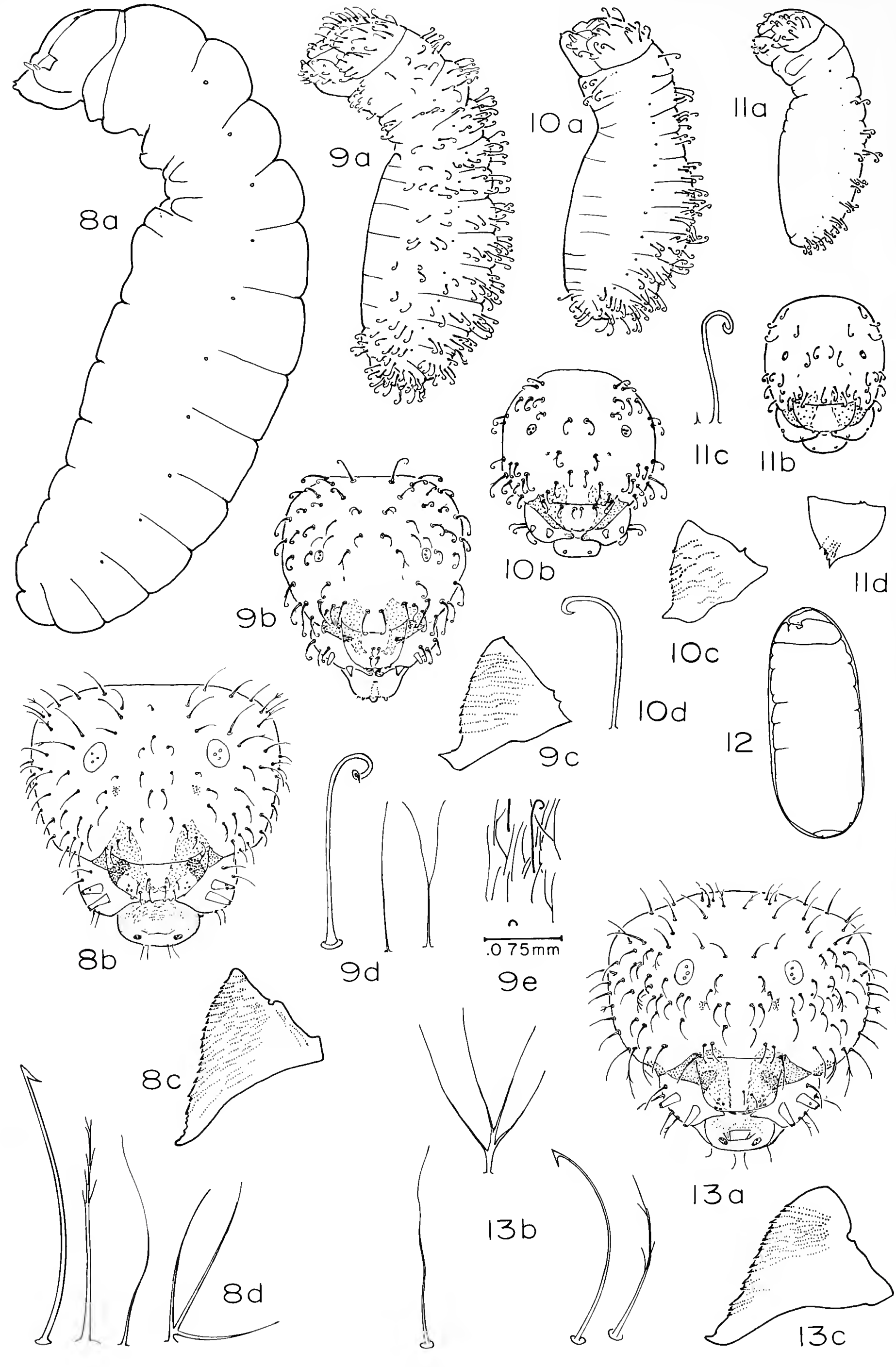
Genus DENDROMYRMEX Emery

Dendromyrmex chartifex (F. Smith)

Figs. 8–13

Description. SUBMATURE LARVA. Length (through spiracles) 3.6–4.3 mm. Profile pogonomyrmecoid; praesaepium present. Anus posteroventral. Spiracles small, decreasing slightly posteriorly. Somites distinct. Integument on venter of anterior somites with spinules in short transverse rows. Body hairs numerous. Of 4 types: (1) 0.05–0.13 mm long, 2- to 4-branched (mostly 2- or 3-branched), evenly distributed; (2) 0.05–0.13 mm long, unbranched, smooth, flexuous, a few on each somite, most numerous on AX; (3) 0.05–0.13 mm long, unbranched, denticulate, a few on each somite; (4) about 0.14 mm long, uncinate, on dorsum of AI–AVII. Head large; cranium transversely subrectangular. Antennae large; just above midlength of cranium. Head hairs 0.05–0.125 mm long; mostly smooth, a few with a few denticles. Otherwise similar to *D. fabricii* (Wheeler and Wheeler 1953:201).

THIRD INSTAR LARVA. Length (through spiracles) about 2 mm. Thorax stout and curved ventrally, abdomen straight and slightly swollen; posterior end rounded. Anus posteroventral. Spiracles minute. Somites distinct. Spinules on venter of T2–AII, dorsum of AVI–AIX and all surfaces of AX. Body hairs numerous. Of 3 types:


8a
9a
10a
11a
11c
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9e
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13a
13b
8d
13c

(1) 0.013–0.1 mm long, very fine, unbranched or bifid, smooth, on all somites; (2) 0.013–0.13 mm long, with stout shaft and curled uncinate tip, on all surfaces of thorax and AVIII–AX, and dorsal and lateral surfaces of AI–AVII; (3) 0.05–0.13 mm long, uncinate, with tip curled and denticulate shaft, on all surfaces of T1–T3. Head large; cranium subhexagonal, about as broad as long. Antenna small, at midlength of cranium, with 3 sensilla each bearing a spinule. Head hairs short, moderately numerous. Of 3 types: (1) 0.06–0.08 mm long, uncinate with curled tip, a few with a few denticles on shaft; (2) about 0.1 mm long, few, bifid; (3) about 0.08 mm long, few, unbranched, smooth. Labrum paraboloidal; chiloscleres feebly developed; anterior surface with 4 hairs and 4 sensilla; ventral surface with 6 projecting sensilla; posterior surface densely spinulose, the spinules minute and in rows radiating from the dorsolateral angles. Mandible camponotoid but with the apex stout, ending in a small short tooth directed medially; feebly sclerotized; stout; anterior and posterior surfaces with moderately numerous rows of minute spinules. Maxilla terminating in a small cone projecting medially and bearing a few rows of spinules; palp paxilliform, with 5 apical sensilla; galea a stout cone with 2 apical sensilla. Labium with a few short transverse rows of minute spinules; palp paxilliform, with 5 apical sensilla; an isolated sensillum between each palp and the opening of the sericteries; the latter a short transverse slit. Hypopharynx spinulose, the spinules minute and in rows radiating from the dorsolateral angles.

SECOND INSTAR LARVA. Length (through spiracles) about 1.6 mm. Thorax stout and bent ventrally; abdomen straight and slightly swollen. Anus posteroventral. Spiracles minute. Somites feebly differentiated. Entire integument spinulose, the spinules minute and in short rows posteriorly, isolated elsewhere. Body hairs sparse, mostly restricted to dorsal surface; 0.06–0.11 mm long; uncinate with curled tip. Head large; cranium suboctagonal, slightly broader than long. Antenna small, just above midlength of cranium, with 3 sensilla. Head hairs moderately numerous (60); 0.05–0.09 mm long; uncinate with curled tip, some with denticles on shaft. Labrum twice as broad as long; chiloscleres lacking; anterior surface with 4 small hairs and 2 sensilla; ventral surface with 4 projecting sensilla; posterior surface densely spinulose, the spinules minute and in rows radiating from the dorsolateral angles, stout, feebly sclerotized, camponotoid with the apical tooth short and with a few rows of minute spinules on anterior and posterior surfaces. Maxilla swollen ventrolaterally; with conical apex directed medially and with a few short rows of spinules; palp

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Figs. 8–13. *Dendromyrmex chartifex.* 8. Submature larva. A, Larva in side view (hairs omitted), ×27; b, head in anterior view, ×50; c, left mandible in anterior view, ×133; d, 4 types of body hairs, ×267. 9. Third instar larva. a, Larva in side view, ×27; b, head in anterior view, ×50; c, left mandible in anterior view, ×133; d, 3 types of body hairs, ×267; e, relation of uncinate and fine body hairs, ×133. 10. Second instar larva. a, Larva in side view, ×27; b, head in anterior view, ×50; c, left mandible in anterior view, ×133; d, body hair, ×267. 11. First instar larva. a, Larva in side view, ×27; b, head in anterior view, ×50; c, body hairs, ×267; d, left mandible in anterior view, ×133. 12. Egg containing larva, ×27. 13. Sexual larva. a, Head in anterior view, ×27; b, 4 types of body hairs, ×267; c, left mandible in anterior view, ×133.

paxilliform with 5 (4 apical and 1 lateral) sensilla; galea a short frustum with 2 apical sensilla. Labium with a few short rows of minute spinules on anterior surface; palp a short paxilla with 5 apical sensilla; an isolated sensillum between each palp and the opening of the sericteries, the latter a short transverse slit.

FIRST INSTAR LARVA. Length (through spiracles) about 1.2 mm. Thorax stout and bent ventrally, abdomen straight; posterior end round-pointed. Anus ventral. Spiracles minute. Four feebly differentiated somites. Body hairs few. Of 2 types; (1) about 0.088 mm long, uncinate with curled tip, limited to dorsal surface of abdomen, more numerous posteriorly; (2) about 0.006 mm long, 1 on each ventrolateral surface of T1–T3. Head large, of same diameter as T1; bulging anteriorly; cranium subcircular in anterior view. Antenna small, with 3 sensilla; at midlength of cranium. Head hairs moderately numerous (44), 0.038–0.088 mm long, uncinate with curled tip. Labrum trapezoidal; anterior surface with 4 hairs and 4 sensilla; ventral surface with 4 projecting sensilla; posterior surface densely spinulose, the spinules minute and in rows radiating from the dorsolateral angles. Mandible feebly sclerotized, semicircular in anterior view, with a short sharp tooth projecting ventrally; anterior and posterior surfaces with a few short longitudinal rows of minute spinules. Apex of maxilla paraboloidal and with short rows of minute spinules; palp an irregular knob with 5 sensilla; galea a stout frustum with 2 apical sensilla. Labium with a few short transverse rows of minute spinules; palp a slightly raised cluster of 5 sensilla; opening of sericteries a short transverse slit. Hypopharynx spinulose, the spinules minute and in rows radiating from the dorsolateral angles.

EGG (containing 1st instar larvae). Ellipsoidal; 0.9 by 0.4 mm.

SEXUAL (removed from cocoon). Length (through spiracles) 6.7 mm. Body hairs of 4 types: (1) 0.05–0.1 mm long, palmately 2- to 5-branched, a few of longest on each somite; (2) about 0.1 mm long, unbranched, smooth, a few on each somite; (3) about 0.1 mm long, uncinate, on dorsum of AI–AVI; (4) about 0.1 mm long, with a few long denticles, a few on dorsum of thorax. Cranium subheptagonal, broader than long. Head hairs moderately numerous (86). Of 2 types: (1) 0.05–0.125 mm long, unbranched, smooth; (2) about 0.055 mm long, few, 2- or 3-branched. Otherwise similar to submature worker.

Material studied. 7 larvae from Panama—Barro Colorado Island, 20-XI-1982, courtesy of Diana E. Wheeler.

Hölldobler and Wilson, 1983: The larvae are used by the workers to supply silk for reinforcing the carton of the nest-walls.

Genus POLYRHACHIS F. Smith

Hölldobler and Wilson, 1983. Colored photograph of a worker of *P.* sp. (cf. *doddi*) using a larva as a shuttle to weave silk for nest construction. SEM of *P.* sp. labium showing opening of silk glands.

Polyrhachis lamellidens F. Smith

Kôriba, 1963: 4 instars, each described. Duration of stages given. Figure 4 first instar larva.

CAUTION: Hairs have been omitted from most drawings of larvae in side view. In *Aphomomyrmex* they become too fine to be shown accurately at this magnification. In *Paratrechina* 5d most hairs have been broken off. In *Dendromyrmex* 8a they are too numerous.

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Received June 6, 1985; accepted August 19, 1985.

J. New York Entomol. Soc. 94(3):342–371, 1986

THE *CHYMOMYZA ALDRICHII* SPECIES-GROUP (DIPTERA: DROSOPHILIDAE): RELATIONSHIPS, NEW NEOTROPICAL SPECIES, AND THE EVOLUTION OF SOME SEXUAL TRAITS

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Abstract.—Seven new species of *Chymomyza* are described: *C. diatropa, C. exophthalma, C. guyanensis, C. jamaicensis, C. microdiopsis, C. mycopelates,* and *C. procnemolita. Chymomyza maculipennis* Hendel is a junior synonym of *C. bicoloripes* (Malloch). Genitalia of male and female *C. bicoloripes* and male *C. albitarsis* (Hendel) are described and those of *C. aldrichii* Sturtevant and *C. procnemoides* Wheeler are figured. A key is provided for the identification of all members of the *Chymomyza aldrichii* species-group. Males of 5 species have conspicuously broadened heads. Synapomorphy distributions suggest that this trait evolved independently twice, in quite different manners. Spines on the male prothoracic femora evolved less dramatically and have been lost in *C. bicoloripes* and *C. mesopecta* Wheeler. Rampant homoplasy in adult morphology, however, obscures the phylogenetic relationships somewhat and limits definitive statements on the origins of extreme sexual dimorphism in these flies.

Chymomyza Czerny is an undoubtedly monophyletic genus in Drosophilidae based on its many synapomorphies, which were reviewed by Okada (1976). Some of these traits are a proclinate orbital bristle that is situated medial to and between the 2 reclinates, an oviscape with fine setae, male terminalia with prominent gonopods and ventral epandrial lobes, and the males possess strong spines on the ventral surface of the prothoracic or mesothoracic femora. The genus is worldwide in distribution. It is considered one of the advanced genera of Drosophilinae (the Steganinae being the other, but primitive, subfamily), and perhaps originated from *Drosophila* (*Sophophora*) stock in Africa with its sister-group, *Neotanygastrella* (Throckmorton, 1975). Some 43 species are presently known, and many of these were only recently described (Okada, 1976, 1981). Still, in comparison to some other "natural" genera such as *Leucophenga* (158 spp.), the group is dwarfed. Okada (1976) divided *Chymomyza* into the *obscura, fuscimana, costata, procnemis,* and *aldrichii* species-groups, the last 2 being close relatives.

Hendel (1917) described the first neotropical member of the *aldrichii* species-group, and, at that time, it was the second known instance at the generic level of a broad-headed drosophilid male. *Zygothrica dispar* (Wiedemann) (originally as *Achias*) was the species first described with a superficially similar trait. Because of its unusual head shape, Hendel (1917) erected *Zygodrosophila* to ally the specimen with *Drosophila* and with *Zygothrica.* Duda (1927) recognized that "*Zygodrosophila*" *albitarsis* Hendel was probably a *Chymomyza* based only on Hendel's description. In the catalogue of the world Drosophilidae (Wheeler, 1981), *Z. albitarsis* is placed under *Chymomyza,* but an explicit synonymization of *Zygodrosophila* has not been done.

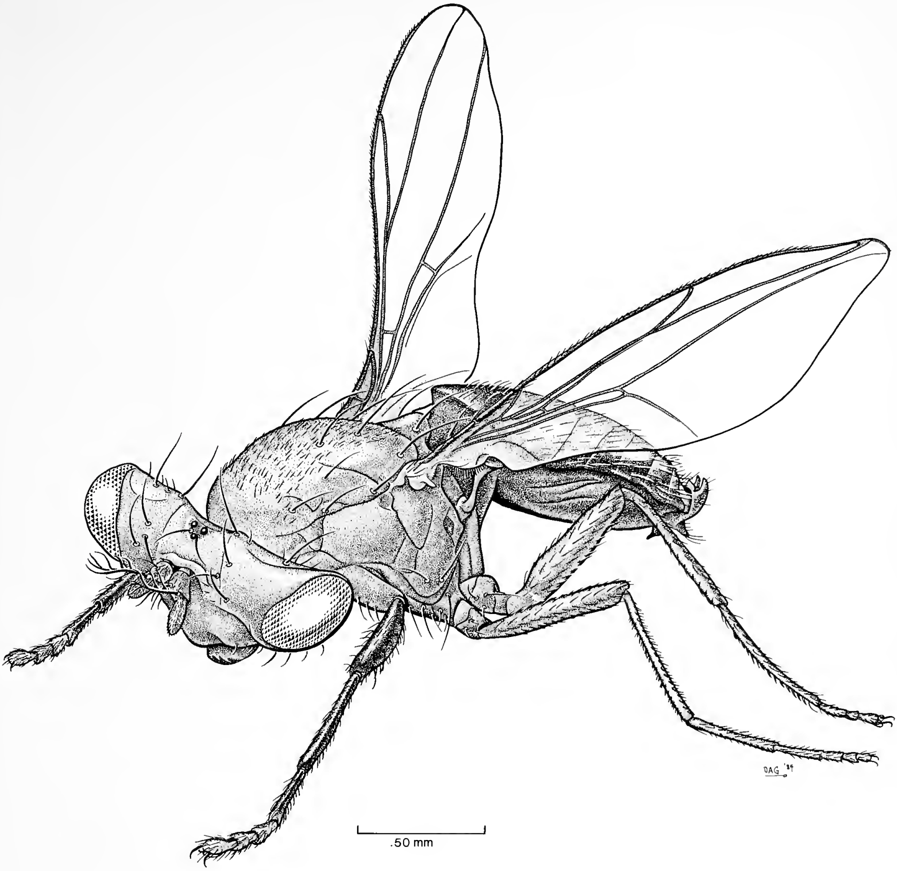


Fig. 1. Habitus, anterolateral view, male *Chymomyza microdiopsis*, n. sp.

Duda (1927) described *C. laevilimbata* and Malloch (1926) described *C. bicoloripes* (as *Drosophila*). In 1936, Hendel described *C. maculipennis*, but Wheeler (1957) mentioned that *C. maculipennis* is probably synonymous with *C. bicoloripes* judging from Hendel's description. Sturtevant (1921) discovered 2 new species with broad heads from Haiti and from British Guyana, but he deferred their descriptions because, as he wrote (p. 61), "it seems better to wait for a study of the male genitalia before attempting to determine the specific limits in the section of the genus to which they belong." Wheeler (1968) described *C. mesopecta*, an unusual member of the species-group, which I will treat here only briefly.

METHODS

Assistance from the following individuals in providing specimens is appreciated (their respective institutions are abbreviated in parentheses and are referred to in the descriptions): Daniel Bickel, Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Ruth Contreras-Lichtenberg, Vienna Natural History Museum (NHMW); Wayne Mathis, Smithsonian Institution, Washington, D.C. (USNM); J. Frank McAlpine, Canadian National Collection, Ottawa (CNC); Kathleen Schmidt, American Museum of Natural History, New York (AMNH). Brian H. Cogan, at the British Museum (Natural History), Paul H. Arnaud, Jr. (California Academy of Sciences, San Francisco), and Francisca Val (Museu de Zoologia de São Paulo) kindly checked through the drosophilids in their respective collections for *Chymomyza.* Throughout the text CUIC denotes Cornell University Insect Collections as a depository. The holotypes of *C. bicoloripes, C. albitarsis, C. procnemoides,* and *C. maculipennis* were studied.

For all species the male and, where available, female terminalia were prepared by clearing them in 10% KOH, washing them in warmed distilled water, passing them through 70% ethanol and then glycerine, and mounting them in glycerine jelly. A Leitz Nomarski optics microscope with camera lucida was used to illustrate most structures. Scanning electron micrographs of the male prothoracic femora were taken at 550× magnification with 5 kV beam current. Specimens were gold-palladium sputter-coated. Several standard measurements were made and some ratios also taken: for the wing, measurements are indicated in Figure 14; those for an analysis of head shapes are given in the discussion section.

Relative phylogenetic relationships are hypothesized based on sets of synapomorphies. Hence, no hypotheses of ancestral relationships are given here. *Chymomyza amoena* (Loew), which belongs to the *fuscimana* species-group (sensu Okada, 1976), was used as an outgroup for deciding the polarity of character states. For some quantitative characters discontinuous states were distinguished where there was an obvious (and, so, probably statistically significant) gap in a morphocline.

My use of morphological terms follows conventions established by McAlpine (1981). This departure from standard *Drosophila* taxonomy is needed to standardize terms for dipterists, but especially for homologizing structures in the terminalia (see Fig. 4). The alternative term paraphysis was used for "paramere" (sensu Griffiths, 1972, 1981) because the latter is a term coined by coleopterists for paraphallic processes at the base of the aedeagus and it is unclear if the 2 structures in beetles and flies are homologous. Oviscape is used here in place of terms in the *Drosophila* literature that refer to the modified lateral surfaces of sternite 8 in females ("egg guides," "ovipositor plates," . . .). It is more specific than "egg guide," which can also refer to the eversible membrane posterior to sternite 8 that often bears fine scales in some drosophilids and actually channels the egg into spaces. "Ovipositor plates" suggests the sternites to be true orthopteroid-type ovipositors, which are appendicular in origin.

All measurements are in millimeters.

RESULTS

I. Species-group diagnosis.

The arista has usually 3 dorsal and 2 ventral branches. The frontal vitta is very finely striate with marks running anteroposteriad, and is golden yellow. Shiny glabrous fronto-orbital plates border the frontal vitta. Eyes are sparsely pilose and brick red. Variable degrees of head broadening in the males of some species occurs, the extent and manner of which is described later. A glabrous ocellar triangle is dark brown to black in the area bordered by the ocelli. The prothoracic coxae and trochanters are relatively light in comparison to the general body color (they are usually white or off-white), and the prothoracic femora, tibiae, and basitarsi are contrastingly dark brown to black. The remaining tarsal segments, 2–5, are white. Meso- and metathoracic legs are similar in color to the body ground color. The entire basicostal, costal, and variable portions of the proximal end of the subcostal cell are infuscated dark-brown to black. The costal vein and usually R_{2+3} and R_{4+5} are much darker than the other veins.

Abdominal tergites are shiny black, and each possesses 3–4 rows of fine long setae arranged transversely. Terminalia are very diagnostic and can be polymorphic, especially for the males. Male terminalia are large and, when not retracted into the eighth abdominal segment, are usually slung ventrally in the manner of many dolichopodids. The aedeagus is prominent, bilaterally symmetrical and compressed, particularly the distiphallus, which is usually bulbous in lateral view compared to the rest of the aedeagus. The oviscape and spermathecae do not appear distinctive among other *Chymomyza* groups, although they can vary among species. Neotropical members of the group are generally quite small, being about ½ the size of some common nearctic species such as *C. amoena* (Loew) and *C. aldrichii* and they resemble in habitus the North American species *C. procnemoides.* Very little sexual dimorphism in size exists; in 3 of the species (*C. guyanensis,* n. sp., *C. exophthalma,* n. sp., and *C. procnemolita,* n. sp.) females are about 10% larger than the males.

II. Key for the identification of males and, where applicable, females of the *Chymomyza aldrichii* species-group members. Final identification often requires examination of some microscopic features of the male and female terminalia (see Figs. 2–12, 13a–h).

1. Entire body dark brown to black 2
– Ground color of head and thorax yellow-orange to light brown 3
2. Eight rows acrostichal setulae present; North America .... *aldrichii*
– Six rows acrostichal setulae present; South and Central America .... *laevilimbata*
3. Femoral spines of male prothoracic legs absent (Fig. 15a); South America 4
– Femoral spines of male prothoracic legs present (Figs. 15b–h) 5
4. Males femoral spines only on mesothoracic legs .... *mesopecta*
– Male femoral spines absent on pro- or mesothoracic legs; crossveins dm-cu infuscated (Fig. 14B) .... *bicoloripes*
5. Ventral lobe of male epandrium with apex broader than the length of the lobe (Fig. 12); spermatheca having scale-like exterior (Fig. 13g); North America .... *procnemoides*
– Not with above characteristics; all neotropical forms 6
6. Face with a distinct, dark brown border on the anterior margin (Fig. 17); male eyes ventrally elongate, or variable for this trait 7
– Face unicolorous yellow, with no distinct dark marking on anterior margin of the face 8
7. Pleura brown; male distiphallus strongly hooked (Fig. 4); Jamaica .... *jamaicensis*
– Pleura similar in color to the yellow-orange notum; male terminalia variable but always with a club-shaped gonopod bearing 2 strong, lateral setae (Fig. 3); distiphallus rounded; widespread in Central and South America .... *diatropa*

8. Male head obviously broadened (Fig. 17) 9
– Male head width the same or only slightly broader than that of thorax 11
9. Head broadening due to ventral expansion of eyes (as in *C. diatropa, C. jamaicensis*: Fig. 17); distiphallus apically truncate (Fig. 7); known only from a single male from Paraguay .... *albitarsis*
– Male heads broadened by an expansion of the fronto-orbital and parafacial plates; distiphallus apically rounded 10
10. Anterior reclinate orbital seta below line extending across dorsal margin of scape; 2 rows of profemoral spines undifferentiated (Fig. 15d); hypandrium uncleft, cercus strongly pointed (Fig. 2); Cuba .... *microdiopsis*
– Anterior reclinate orbital situated above line extending across dorsal margins of scapes; ventral row of male profemoral spines shorter and thinner than those in medial row; cercus rounded (Fig. 10); Panama to Peru, Trinidad .... *exophthalma*
11. Six to 7 rows acrostichal setulae present; proclinate orbital setae end lateral to middle of pedicels (Fig. 17) .... *mycopelates*
– Eight rows acrostichal setulae present; proclinates end at middle of pedicel (Fig. 17) 12
12. Nine to 11 prensisetae on surstylus; setae on ventral lobe of epandrium are relatively short (Fig. 8); distiphallus without a lateral knob .... *guyanensis*
– Seven to 8 prensisetae on surstylus; ventral lobe of epandrium with long apical setae; distiphallus with a lateral knob (Fig. 5) .... *procnemolita*

III. Species descriptions. The order in which they are presented here reflects their phylogenetic positions (Fig. 16).

The *mycopelates* lineage

Chymomyza mycopelates, new species

Figs. 11, 13e, 15h, 17

Description. Head light brown, frons and face glabrous. Light brown on oral margin of face near eyes. Three dorsal and 2 ventral aristal rays, flagellomere I light brown. Lunule and surrounding region dull, light yellow. Eyes bare. Well-developed vibrissa present, subtended by 5–6 setae decreasing in size posteriad. One genal and 1 subgenal seta present. Anterior reclinates above line extending across dorsal margin of pedicels. Proclinates closer to anterior reclinates than to posterior reclinates. Inner verticals and posterior reclinates longest setae on head; anterior reclinates and proclinates shortest. Fronto-orbital plates not extended beyond middle of pedicel. Anterior reclinate, posterior reclinate and inner vertical setae on each side of head in line with each other. Posterior reclinate ½ the distance between anterior reclinate and inner vertical. Head width to total thorax length ratio (HW/ThL) = 0.80 (5♀♀), 0.83 (5♂♂), total thorax length (ThL) = 0.81 (5♀♀), 0.83 (5♂♂).

Notum and pleura light orange, but darker to almost light brown on subscutellum and katepisternum. Sternum light yellow to off-white. A mean of 10 (range: 8–13) spines in medial row and 11 (9–13) in the ventral row of male prothoracic femora. Medial row spines about ¾ the length of the other spines. Forecoxa with 5 prominent distal setae. One postpronotal seta present; pair of lateral prescutellar setae about twice the length of acrostichal setulae. Dorsocentral setae and anterior scutellars in line with each other. Wing measurements: C.I. = 1.03 (5♂♂ + 5♀♀); 4-V index = 2.55 (5♀♀), 2.73 (5♂♂); 4-C index = 1.75 (5♀♀), 1.89 (5♂♂).

Female with narrow, somewhat elongate oviscape possessing 4 terminal setae and row of evenly spaced setae (usually 6) on ventral margin. Spermatheca large and conspicuously ribbed on basal third of the capsule. An introvert extended about 0.8 the capsule length, and an inconspicuous apical indentation present. Male genitalia conspicuously unique: cercus small and evenly rounded in profile, epandrium high, its length less than ½ its height. Inner wall of epandrium bears 3 straight, fine setae. Surstylus with 8 prensisetae, all rather short. Ventral epandrial lobe narrowed apically, setae on apical quarter of lobe short and fine (about 20 present). Ventral margin of lobe bearing a row of 20–25 very long setae, their length 3 times or more the lobe width. Epandrial lobe bearing sparse vestiture of microtrichia on base. Ventral margin of hypandrium strongly cleft; paraphysis indistinct, bearing 3 short sensilla. Gonopod of moderate size and with 1 strong, dorsally projecting, scale-like seta situated preapically and 4 finer ones of equal length evenly spaced on dorsal margin. Distiphallus curved upward, with lateral knob and a thinner one on ventral margin. Apex of distiphallus membranous and can appear torn: it, like that of *C. guyanensis,* probably eversible. No vestiture present on distiphallus. Main shaft of endophallus very thin, its width about ⅓ that of ventral epandrial lobe. Aedeagal apodeme rudimentary and bearing no lateral flanges: attached to a broadly triangular gonopodal apodeme.

Holotype. ♂, COSTA RICA: La Francia, XI-14-52, Goodyear Plantation, J. B. Carpenter (USNM). Additional label: "feeding on fungus *Ceratostomella fimbriata* on fresh cut logs of *Hevea brasiliensis.*"

Paratypes. 24♂♂ and 9♀♀, same locality and date as the holotype (all USNM).

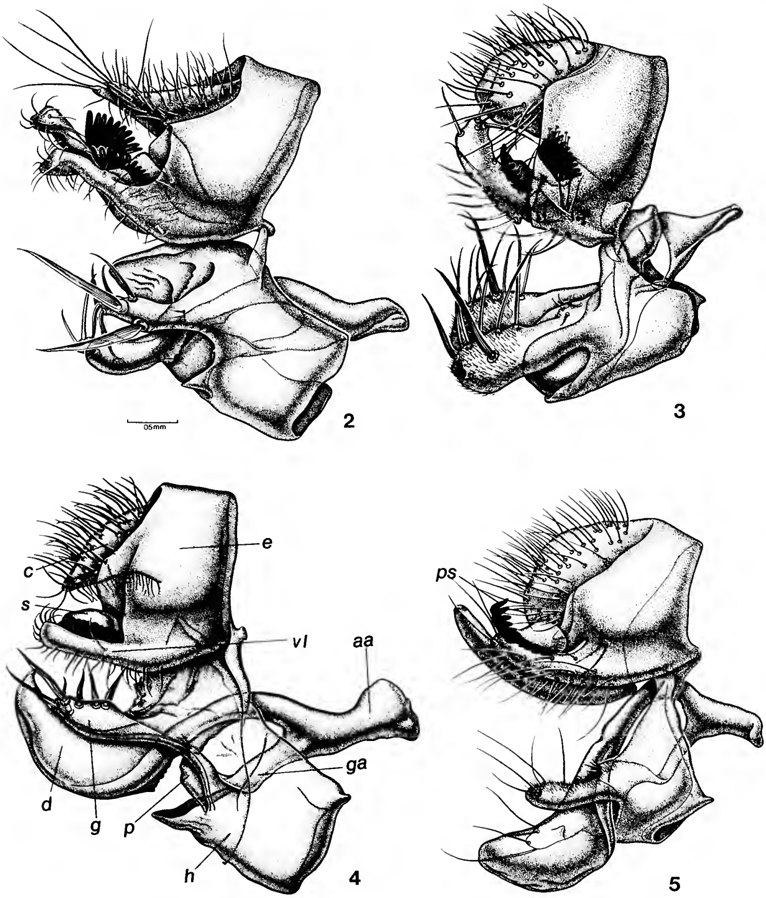
Etymology. Gr., "fungus-approacher," because of its feeding habit.

Chymomyza microdiopsis, new species

Figs. 1, 2, 13f, 14C, 15d, 17

Description. Head and thorax light orange, ventral portions of head light yellow to almost white. Four dorsal and 2 ventral aristal branches. A vibrissa each subtended by 5–7 setae of equal length. Proclinate orbital setae end at middle of pedicel. Anterior reclinate, posterior reclinate and inner verticals in line with each other. Anterior reclinates attached at level of anterior margin of scape. Inner verticals longest setae on head and ocellars are shortest. HW/ThL = 1.38 (10♂♂). One large postpronotal seta and 6 rows of acrostichals. Forecoxa with 6 (5–8) strong, equal-sized setae distad. Eight to 10 (mean of 9) spines per row on male prothoracic femora. Mesothoracic coxa with 5 setae, metathoracic coxa with 1. ThL = 0.83 (10♂♂), 0.98 (1♀). Wing measurements: C.I. = 1.18 (10♂♂, 10♀♀), 4-V index = 2.73 (10♂♂), 4-C index = 1.78 (10♂♂).

Oviscape narrowed apicad, with 5 long apical setae and 3 shorter ones. Hypoproct modified internally into a pair of broadened flanges. Spermatheca of intermediate size (about 60 μm); an introvert present. Spermathecal capsule with smooth surface. Male cercus apically pointed and with 2 very long apical setae. Ventral lobe of epandrium apically knobbed, with 10–12 setae. Surstylus with usually 10 prensisetae, sometimes 11; many fine setae on medial surface of lobe. Dorsal margin of epandrium narrow in profile, hypandrium large. Paraphyses small and with 3 short, fine sensilla. Gonopod with 2 large scale-like setae and 4 smaller, apical ones. Gonopod devoid of microtrichia. Distiphallus narrow in profile, apically rounded, ventral margin with



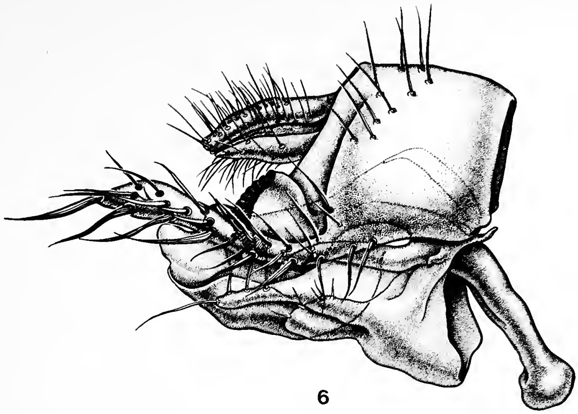
Figs. 2–12. Male terminalia of *Chymomyza aldrichii* species-group members, lateral view, all to the same scale. 2. *C. microdiopsis.* 3. *C. diatropa.* 4. *C. jamaicensis.* 5. *C. procnemolita.* 6. *C. bicoloripes.* 7. *C. albitarsis.* 8. *C. guyanensis.* 9. *C. aldrichii* (ventrolateral view of hypandrium and associated appendages). 10. *C. exophthalma.* 11. *C. mycopelates.* 12. *C. procnemoides.* Abbreviations: aa, aedeagal apodeme; c, cercus; d, distiphallus; e, epandrium; g, gonopod; ga, gonopodal apodeme; h, hypandrium; p, paraphysis; ps, prensisetae; s, surstylus; vl, ventral epandrial lobe.

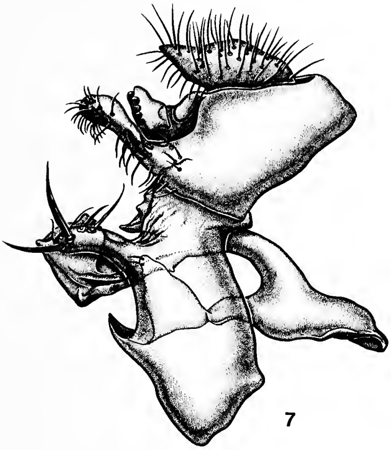
approximately 8 blunt serrations along length with a larger knob anteriad. Basiphallus of medium height; lateral flanges well-developed on aedeagal apodeme. Apex of distiphallus devoid of microtrichia.

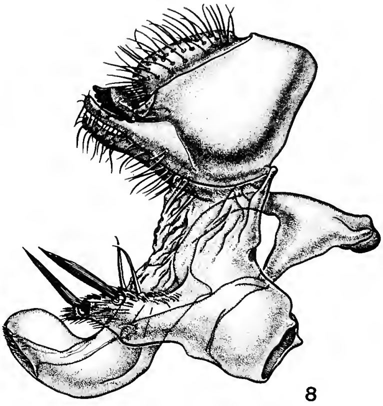
Holotype. ♂, CUBA: Santa Clara Province, San Juan Mountains, Jan.–Feb. 1927, C. T. and B. B. Brues (USNM).

Paratypes. 11♂♂ (MCZ), 15♂♂ and 1♀ (USNM), all with same label data as holotype.

Etymology. Gr., "tiny diopsid," after its most striking feature that is common in a distantly-related family.





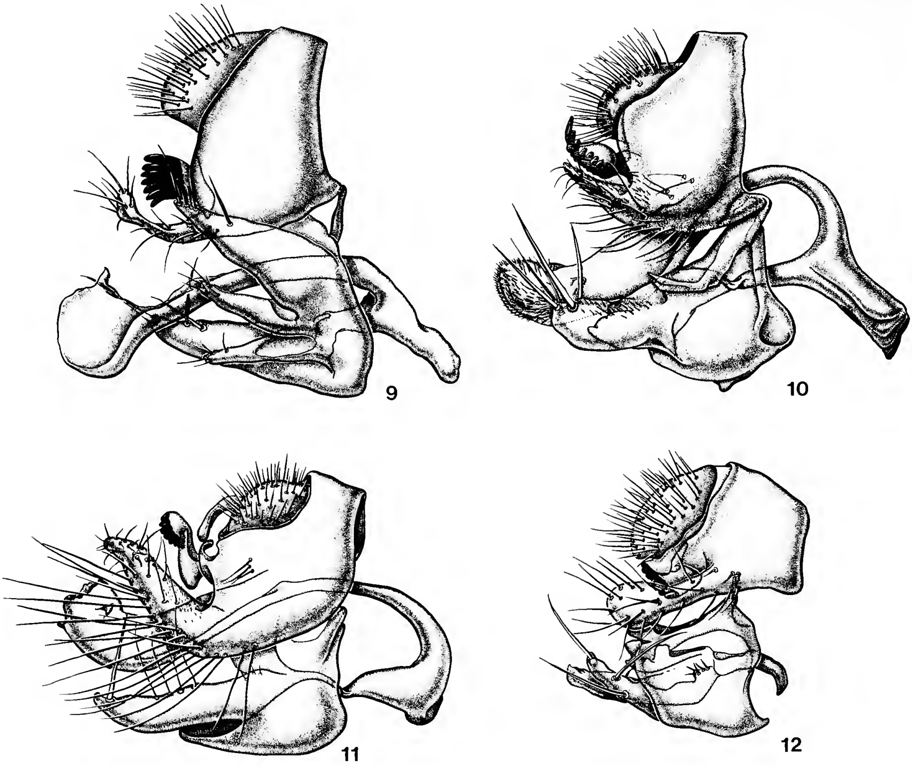


Figs. 6–8. See caption on page 348.

Chymomyza exophthalma, new species

Figs. 10, 13h, 17

Description. Head yellow, with no conspicuous markings. Male head variably broadened due to expanded fronto-orbital and parafacial plates. Inner margins of eyes parallel and not divergent dorsally. Three dorsal and 2 ventral aristal branches, the third dorsal one very close and just distal to first ventral one. Proclinates ending just mediad of pedicel center and their bases lying equidistant between anterior and posterior reclinates. Anterior reclinates in line with dorsal margins of scapes. Inner vertical medial to line extending from anterior to posterior reclinates. Inner verticals the longest head setae. Fifteen to 17 postocular setae per side. Postocellars relatively long, lengths about that of paraverticals. A heavy vibrissa subtended on each side



Figs. 9–12. See caption on page 348.

by 4 shorter setae of equal thickness. One genal and 1 subgenal seta. HW/ThL = 1.07 (5♂♂), 0.90 (5♀♀).

Thorax, particularly pleura and sterna, darker than head. Subscutellum light brown. Six rows evenly spaced acrostichals. One postpronotal seta, the length of the 2 lateral prescutellars about twice that of acrostichals. Dorsocentrals and anterior scutellars in line with each other. Prothoracic coxa with 4–5 heavy, long setae distad; also several long, finer setae. Male prothoracic femur with 9–10 spines in medial row, their lengths about equal to ¾ femur width. Seventeen shorter spines in ventral row. Twelve fine setae in lateral row bordering the ventral pollinosity. Mesothoracic coxa with 2 long setae and metathoracic with 1. Metathoracic tibia brown, but not as dark as fore femora and also gradually lighter distad. Wing measurements: C.I. = 1.16 (5♂♂), 1.28 (5♀♀); 4-V index = 2.40 (5 ♂♂), 2.48 (5♀♀); 4-C index = 1.65 (5♂♂), 1.55 (5♀♀).

Spermatheca trapezoidal in profile to almost oval, base abruptly funneled. Apical indentation inserted into open apex of introvert. Oviscape long and with 5 long and 2 shorter apical setae. Introvert slightly ribbed. Male terminalia similar to those of *C. procnemolita* except for following characteristics: 11 prensisetae per surstylus; 4 long fine setae on inner wall of epandrium; ventral lobe of epandrium apically pointed and setae on it diminished in length apicad; dense microtrichia on distiphallus; 2 sensilla on prominent, pointed paraphysis; paraphysis attached proximad to a sclerotized, sharp lobe; gonopod about as high as distiphallus and with 2 prominent, thick setae and 3 thinner ones; gonopodal apodeme separated from main endophallal shaft by wide curvature; aedeagal apodeme robust and as long as ventral margin of hypandrium. Like *C. procnemolita,* distiphallus with a lateral knob, an uncleft hypandrial margin, a rounded cercus, and the distiphallus of a similar shape.

Holotype. ♂, PANAMA: Canal Zone, Barro Colorado Island, 26 May 1961, S. B. Pipkin (USNM).

Paratypes. PANAMA: Canal Zone, Barro Colorado Island, 19–26 May 1961 (4♂♂, 4♀♀) and 10 May 1961 (1♀), 10 September 1960 (1♀), S. B. Pipkin (all USNM). PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado IX/19–X/10/84, 12°12′S, 69°16′W, 290 m, D. A. Grimaldi (2♂♂, 2♀♀) (CUIC). TRINIDAD: Arima, 800–1,200 ft, 10–22 Feb. 1964, J. G. Rozen & P. Wygodzinsky (3♂♂, 2♀♀) (AMNH).

Etymology. Gr., "bulging-eyed," in reference to the frontward appearance of the head.

Comments. Some behavioral notes were taken on this species and are given in the discussion section under Leg Ornamentation and Reproductive Behavior.

The *diatropa-guyanensis* lineage

Chymomyza bicoloripes (Malloch, 1926), **New Combination**

Figs. 6, 13a, 14B, 15a

Drosophila bicoloripes Malloch, 1926:31. Holotype: ♂, PANAMA: Canal Zone. Las Cascadas. A. H. Jennings, coll. Type no. 28467 (USNM).

Chymomyza maculipennis Hendel, 1936:7. Holotype: ♀, BRAZIL: Amazonas-Dampfer, Gurupa-Almeirim, 29.V.27, Zerny. (NHMW). **New Synonymy.**

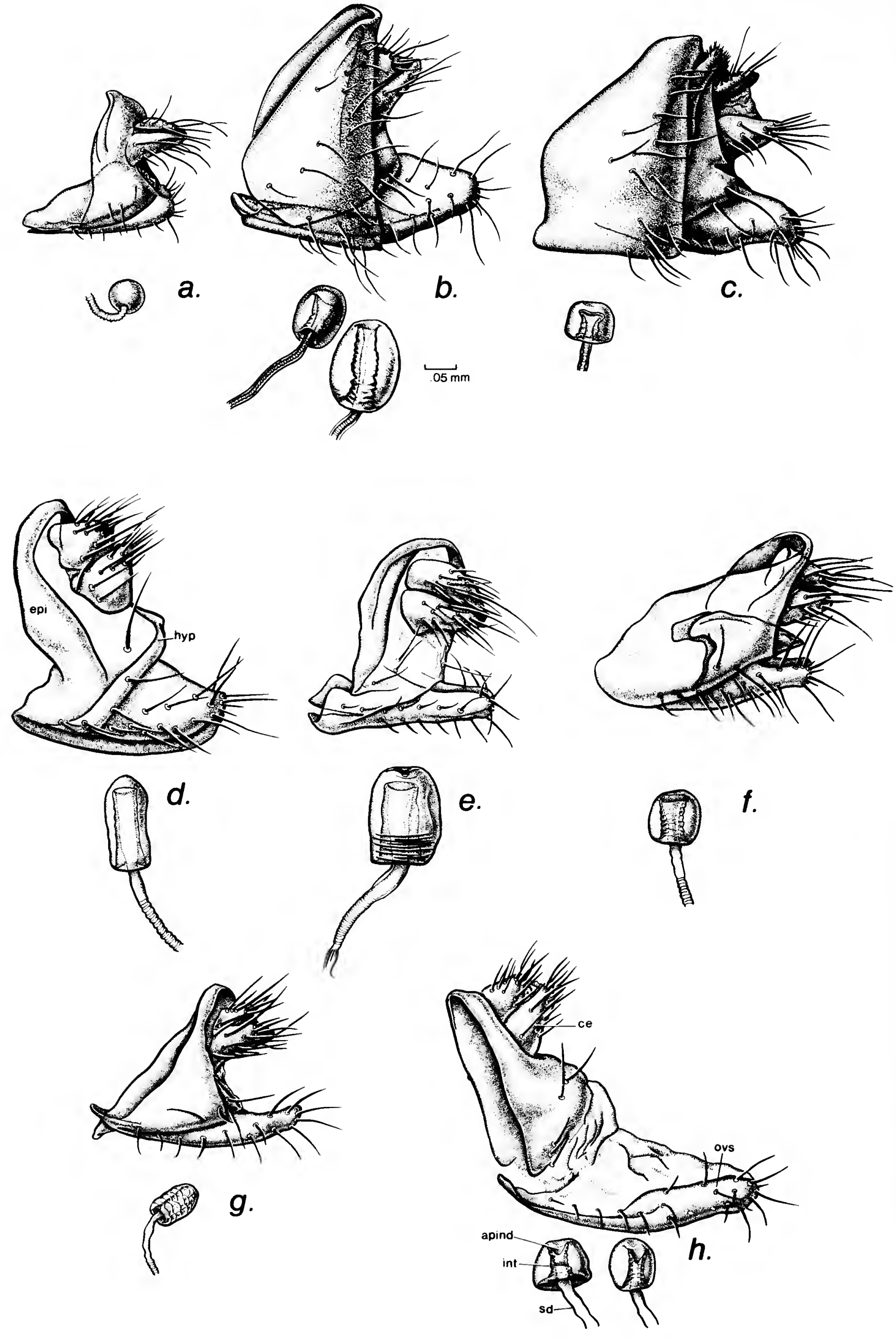
Chymomyza bicoloripes: Wheeler, 1957:103.

Since Malloch and Hendel described the habitus, I deal with it here only briefly and concentrate on the very diagnostic terminalia.

Description. Arista with 4–5 dorsal and 2 ventral rays. Orbitals in line with each other and with inner verticals. Eyes moderately pilose. Inner vertical setae longest, ocellars shortest setae on head. A large vibrissa subtended on each side by 6 smaller setae, their lengths about ½ that of vibrissa. Four subgenal setae and 10 postoculars per side of head. Six rows of acrostichal setulae. Male without pro- or mesothoracic femoral spines. Wings with distinct brown cloud over end of R_{4+5} extended to distal end of M or just distad; prominent infuscation over crossvein dm-cu. Wing measurements: C.I. = 1.18 (6♂♂), 1.30 (2♀♀); 4-V index = 1.95 (6♂♂), 1.87 (2♀♀); 4-C index = 1.38 (6♂♂), 1.28 (2♀♀). Other measurements: HW/ThL = 0.80 (6♂♂), 0.73 (2♀♀).

Female terminalia relatively small, oviscape blunt, with 5–6 short, curved setae/sensilla on ventral margin and evenly spaced from each other. Apex with 2 short, peg-like sensilla and 3–4 longer setae, the 2 thick ones resembling sharp scales. Spermathecae small, spherical, heavily sclerotized, without an introvert.

Male terminalia large, most portions elongate. Cercus and dorsal margin of epandrium elongate in profile. Dorsolateral surfaces of epandrium with 9–10 strong setae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per side. Thirteen to 14 short prensisetae per surstylus. Ventral epandrial lobe narrow and very elongate, length about twice that of cercus. Strong, straight setae along its length, terminal ones best developed. Distiphallus enlarged, scoop-like, and with curved apical margin. A very elongate hypandrium not ventrally cleft. Several processes lateral to aedeagus present: A well-developed paraphysis with 5 sharp sensilla on dorsal surface; gonopod reduced and with thin apical seta and 3 evenly spaced setae of equal length on dorsal margin; the most lateral process, between ventral epandrial lobe and gonopod, forming a direct extension of that part of hypandrium connecting to gonopod. This thin lobe probably a gonopod derivative. Very little curvature in main shaft of basiphallus, aedeagal apodeme long and without lateral flanges.

Material examined. Besides the two type specimens mentioned above, the following were also studied: COSTA RICA: La Francia, Goodyear Estate, VI-1-52, J. B. Carpenter, 52-6587 (USNM). GUYANA: Tukeit (Falls), 20.VII.1911, "L.4.b." on back of label (1♀) (AMNH). PANAMA: Almirante, Bocas del Toro Pr., F. S. Blanton, Jan. 1953 (1♂), and Nov. 1952 (1♂) (USNM); Darien Province, Jaque, 28 July 1952, F. S. Blanton (2♂♂) (USNM). TRINIDAD: Arima, Blanchisseuse Rd., 2,000′, 28–31 Jan. 1982, M. S. Adams (1♀) (CUIC). VENEZUELA: Bolivar, Rio Karui, 16 mi N Kavanayen, 1,000 m, 10–11 Aug. 1970, R. E. Dietz (1♂) (USNM).

Comments. This species is a very derived member of the *guyanensis-diatropa* lineage. Besides other specimens that are in the USNM collection from Turrialba, Costa Rica, Wheeler (1957) mentioned that he had seen specimens collected on Barro Colorado Island, Panama, "off a fresh-cut log" and at Villavicencio, Columbia. This species is widespread throughout Central America and probably tropical areas of South America but it is not known to reside on any of the Antilles.

Chymomyza procnemolita, new species
Figs. 5, 13b, 14A, 15b, 17

Description. Male head generally narrow, broader in some specimens than others. Heads in both sexes very flat and with elongate profile. Arista with 3–4 dorsal branches (terminal one very small) and with 2 ventral ones. Ocellar triangle varying from slightly darker than yellow head color to dark brown. Inner vertical slightly mediad of line extending from anterior to posterior reclinate orbital setae. Anterior reclinates level with dorsal margins of scapes. Proclinates lying ½ distance between anterior

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Fig. 13. Female terminalia (lateral views) and spermathecae, all to the same scale. Orientations of some structures, especially the epiproct in relation to the hypoproct, were not standardized. They are shown here mostly as a reference for the differences in relative sizes of spermathecae, oviscapes, and associated sclerites. a. *C. bicoloripes*; b. *C. procnemolita* (left spermatheca from Trinidad specimen, right one from Costa Rica); c. *C. diatropa*; d. *C. aldrichii*; e. *C. mycopelates*; f. *C. microdiopsis*; g. *C. procnemoides*; h. *C. exophthalma* (left spermatheca from Panama specimen, right one from Peru). The structures are arranged in order from blunt (a) to pointed (h) oviscapes. The oviscape of *C. exophthalma* is shown entirely everted. Abbreviations: apind, apical indentation; ce, cercus; epi, epiproct; hyp, hypoproct; int, introvert; ovs, oviscape (=sternite 8); sd, spermathecal duct.

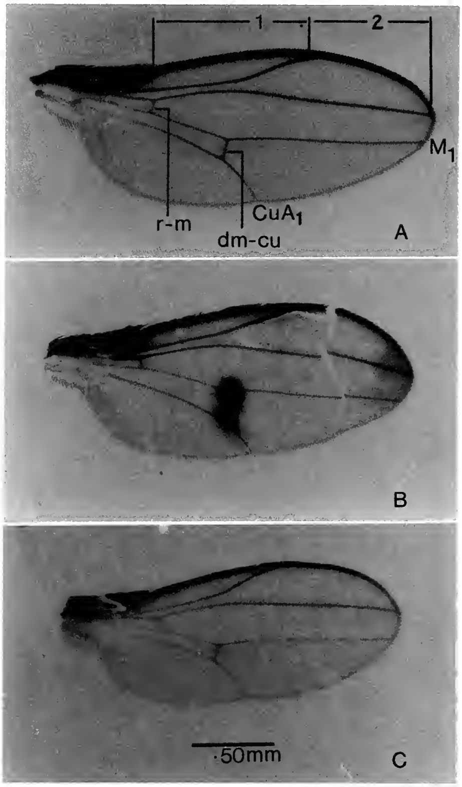


Fig. 14. Wing photographs of A. *C. procnemolita* female; B. *C. bicoloripes* female; C. *C. microdiopsis* male. Measurements: Costal Index (C.I.) = segment 1/segment 2; 4-V index = length from dm-cu to end of M_1/length from r-m to dm-cu; 4-C index = segment 1 length/length of segment from r-m to dm-cu.

and posterior reclinates, or slightly closer to anterior reclinates. Proclinates terminating at inner margins of scapes. Strong, forward-projecting vibrissa subtended on each side by 4–6 setae about ½ its length. One strong genal and 1 thinner but equally long subgenal seta per side. Eleven to 14 postoculars (usually 12) present per side; always 2 paraverticals per side, their length less than twice that of postocellars. HW/ThL = 0.94 (8♂♂), 0.91 (9♀♀); 2♂♂ from Panama with HW/ThL = 0.95 and 2♀♀ = 0.90; ThL = 0.76 (10♂♂), 0.86 (11♀♀).

Female terminalia diagnostic. Broad oviscape, apically truncate with 4 long and 3 shorter apical setae. Spermathecal height 1.5 × that of width. No apical indentation, but introvert extending entire length of capsule. Half of introvert near spermatheca opening with ribs, and, in a Costa Rican specimen, the ribs extended to introvert apex but here less distinct. Costa Rican specimen with enlarged spermatheca, oviscape similar to that of figured Trinidad specimen (Fig. 13b).

Like some other species in group, male terminalia varying in amount of vestiture on ventral epandrial lobes and gonopods and of microtrichia on distiphallus. Cercus broadly rounded in profile and each surstylus with 7–8 prensisetae of moderate length. About 8 fine setae along ventral portion of cercus underneath epandrium. Ventral epandrial lobe with 3 strong, very long apical bristles and 15–20 shorter ones over remainder. Sparse microtrichia sometimes present on dorsal surface of lobe. Two setae on internal wall of each side of epandrium, lengths about that of epandrial lobe setae. Distiphallus well sclerotized but slightly membranous ventrally, lateral knob present. Distiphallus apex bare or with very sparse microtrichia. Main endophallal shaft extended out straight from aedeagal apodeme, then bent sharply ventrad and lying parallel with gonopodal apodeme. Paraphyses distinct, but still just raised portions of gonopod bases, each with 2–3 short, straight sensilla. Gonopod with dense vestiture of microtrichia, especially on dorsal surface. Ventral margin of hypandrium short and uncleft. No lateral flanges on aedeagal apodeme.

Holotype. ♂, TRINIDAD: Arima, Blanchisseuse Road, 2,000′, 28–31 January 1982, Morton S. Adams (USNM).

Paratypes. COSTA RICA: La Suiza, July 1926, Pablo Schild (1♀) (USNM). PANAMA: David, Chiriqui, 2,200′, 24 July 1964, A. Broce, light trap (1♂, 2♀♀) (USNM). TRINIDAD: Arima, Blanchisseuse Rd., 2,000′, 28–31 Jan. 1982, M. S. Adams (4♂♂, 11 ♀♀) (USNM, CUIC).

Etymology. Gr., derived from *Chymomyza procnemoides,* as "plain procnemoides," or, literally, "plain swallower."

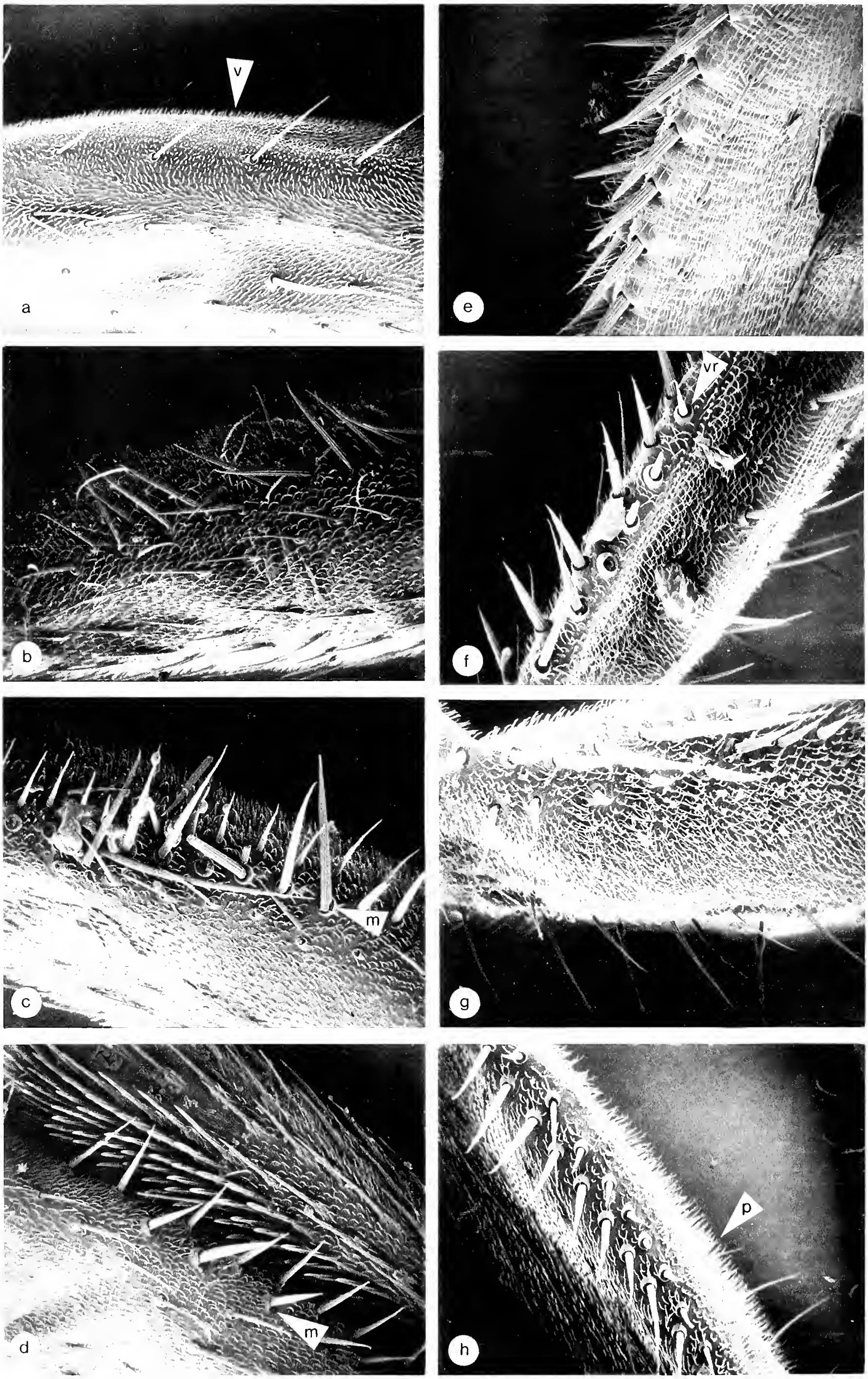
Chymomyza diatropa, new species

Figs. 3, 13c, 17

Description. Male head broadened slightly to not at all. Three dorsal, 2 ventral aristal rays. Proclinates extended to middle of pedicel: bases slightly forward ½ distance between 2 reclinates and just lateral to fronto-orbital sulcus. Posterior reclinate lying ½ distance between anterior reclinate and inner vertical. Anterior reclinate lying far forward: its level on face in line with middle of scapes, sometimes to almost dorsal margin of scapes. Anterior margin of face with dark brown area extended slightly past distal end flagellomere I. Five strong subvibrissal setae, their thickness at most ½ that of vibrissa. Moderately dense, short eye pilosity. Eight to 10 postocular setae per side of head, 2–3 paraverticals (2 always between verticals). Inner verticals and posterior reclinate orbitals longest setae on head; proclinates and genals shortest.

Eight irregular rows of acrostichal setulae. Anterior scutellars in line with dorsocentrals. One large postpronotal seta. Thorax uniformly orange to amber. Prothoracic coxa with 5–6 setae, femur with 7–9 long spines (equal to or greater in length than femur width) in medial row, lateral row with 10 straighter and stouter spines. Mesothoracic coxa with 2 forward-projecting setae, metathoracic coxa with 1–2 setae. Wing measurements: C.I. = 1.09 (5♂♂, Guyana), 1.08 (3♂♂, Costa Rica), 1.32 (1♂, Venezuela), 0.99 (3♀♀, Guyana); 4-V index = 2.62 (6♂♂, Guyana), 2.42 (3♂♂, Costa Rica) and 2.52 (3♀♀, Guyana); 4-C index = 1.90 (6♂♂, Guyana), 1.70 (2♂♂, Costa Rica) and 1.86 (3♀♀, Guyana). Other measurements: HW/ThL = 1.07 (9♂♂, Guyana), 0.80 (5♂♂, Costa Rica), 0.85 (5♀♀, Guyana); ThL = 787 μm (16♂♂), 790 μm (5♀♀).

Male terminalia, but not female, somewhat variable. Eight to 9 prensisetae per surstylus, cercus apically rounded but ventrally flat in profile. Ventral epandrial lobe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straight or slightly upcurved, bearing 20–30 long setae (greater in length than width of ventral epandrial lobe), some hidden beneath epandrium. Hypandrium deeply cleft ventrally. Gonopod always broad laterally, apex sometimes twice the height of base. Gonopod with 2 scale-like setae laterad, 4–7 thinner dorsal setae. All gonopod setae upright, projected dorsad. Gonopod sometimes devoid of microtrichia, but usually with varying amounts on dorsal surface (perhaps some rubbed off during mating). Endophallus profile not emarginate, but wrinkled proximad due to membranous surface. Ventral tooth of phallapodeme absent, or, when present, minute and very close to crotch of basiphallus and aedeagal apodeme; aedeagal apodeme short, narrow in profile. Paraphysis rudimentary, a lump on medial surface of gonopod, with 3 short, sharp sensilla. Distiphallus without a lateral knob and without vestiture. Female with intermediately-broadened oviscape curved slightly downward. Epiproct with many fine setulae on dorsal surface. Spermatheca as high as broad; introvert structure invariant.

Holotype. ♂, Tukeit, British Guyana, 20.VII.1911. Back of label: "L.4.b." (AMNH).

Paratypes. 9♂♂, 5♀♀, Tukeit, British Guyana, 20.VII.1911. Also on the back of each label is written "L.4.b." (AMNH).

Other material examined. COSTA RICA: Turrialba, XII-6-52, J. B. Carpenter (on *Hevea braziliensis* tap panels) (5♂♂) (USNM). DOMINICA, WEST INDIES: Clarke Hall, July 1964, T. J. Spilman (light trap) (1♀); Bells, 20 September 1965, D. L. Jackson (1♂) (USNM). ECUADOR: Puyo, 16 May 1977, P. J. Spangler & D. R. Givens, #51 (1♀) (USNM). PANAMA: Chiriqui, Chiriqui Viejo Riv., El Volcan, 5,280′, 22 July 1966, A. Broce (light trap) (1♂) (USNM). UNITED STATES: Miami, Florida, 28 January 1969, J. C. Buff (light trapping) (1♂) (USNM). VENEZUELA: Aragua, Rancho Grande, 1,100 m, I. '66, S. S. & W. D. Duckworth (1♂) (USNM).

Etymology. Gr., "variable," because the morphological variation found in this species exceeds that of any other in the group.

Comments. This is the most widespread and variable of the neotropical species. Although some specimens seem different enough from the main sample of Guyana specimens as to perhaps represent different species (i.e., the Venezuela and Panama specimens), the male terminal show an obvious overall similarity. The species is distributed from southern Florida and probably most of tropical Mexico, throughout the Greater and some Lesser Antilles, and probably to the southern margin of the Amazon basin. The type-locality, Tukeit, British Guyana, probably refers to Tukeit Falls in the Mazaruni-Potaro District of Guyana (5°13′S, 59°25′W).

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Fig. 15. Scanning electron micrographs of some male *Chymomyza* prothoracic femora (550×, 5 kV), showing the variations in spine structure, number, and positions. a. *C. bicoloripes* (Bolivar, Venezuela); b. *C. procnemolita* (Arima, Trinidad); c. *C. guyanensis* (Tukeit, Guyana); d. *C. microdiopsis* (Santa Clara, Cuba); e. *C. aldrichii* (Pacific Grove, California); f. *C. procnemoides* (Lapeer Co., Michigan); g. *C. amoena* (Guelph, Ontario); h. *C. mycopelates* (LaFrancia, Costa Rica). Abbreviations: m, medial spine row; p, fine ventral pollinosity; v, ventral portion of femur; vr, ventral spine row.

Chymomyza jamaicensis, new species
Figs. 4, 17

Description. Head yellow, anterior margin face dark brown and extended to about distal tip of flagellomere I. Arista with 3 dorsal and 2 ventral branches. Proclinates strongly convergent, ends almost touching. Inner verticals lying mediad of line extending through reclinate setae. Position of anterior reclinate below line extending across dorsal margin of scapes. Seven subvibrissal setae per side of head. Paravertical setae longer than twice postocellar length. Eyes bare, dorsal portion extended outward on elongate fronto-orbital plate with facial portion unmodified and here distance separating eyes about equal to frontal vitta width. Inner vertical seta longest, proclinates shortest ones on head. Pleura chocolate brown, gradually lightened posteriad; metakatepisternum light (same color as coxa), notum and scutellum red-brown, and subscutellum same color as pleura. One large postpronotal seta, 8 rows of acrostichals. Forecoxa with 6 prominent setae. Forefemur with 15 spines in medial row (ventral row obscured). Mesothoracic coxa has 4 and metathoracic coxa with 1 seta. All portions of meso- and metathoracic legs orange. Wing measurements: C.I. = 1.07, 4-V index = 2.98, 4-C index = 2.02. Other measurements: HW/ThL = 1.29, ThL = 880 μm.

Male terminalia with cercus apically pointed but dorsally rounded in profile. Numerous fine setae on ventral surface of cercus. Ventral epandrial lobe straight, ending bluntly but not knobbed. Ten prensisetae per surstylus, dorsal margin of epandrium short. Well-developed paraphysis bearing 3 apical, sharp sensilla. Distiphallus large, curved sharply dorsad at apex, and ventral margin with 6 blunt serrations and large knob between them and basiphallus. Distiphallus devoid of microtrichia. Gonopod base narrow, distal portion with 2 large, apical scale-like setae and 4 smaller, equal-sized setae medially. Gonopodal apodeme robust. Basiphallus high in profile and without lateral flanges. Gonopod devoid of microtrichia.

Holotype. ♂, JAMAICA: Hardware Gap, 4,000′, VII-6-66, Howden and Becker (CNC).

Etymology. Latin, "from Jamaica," in regard to the type locality.

Comments. This description is based on the holotype, which is the only specimen known for the species.

Chymomyza guyanensis, new species
Figs. 8, 15c

Description. Head narrow, face elongate. Inner margins of eyes meeting outer margins of flagellomere I. Arista with 3 dorsal and 2 ventral branches. Proclinate orbital setae terminating at middle of pedicels. Head yellow, except for darkened ocellar triangle. Fronto-orbital plates extended slightly beyond proclinate orbitals. Twelve to 16 postocular setae per side of head; postocellars minute. Eye pilosity short and sparse, especially anterior part of eye. Anterior reclinate, posterior reclinate, and inner vertical setae in line with each other on each side of head. Proclinates much closer to anterior reclinate than to posterior reclinate. Anterior reclinate situated above line extending across dorsal margins of scapes. A strong, forward-projecting vibrissa subtended on each side by 4–6 equally thick, shorter setae. Two thin, straight genals, 2 paraverticals, length of latter about equal to distance between inner and outer vertical setae.

Eight rows of evenly spaced acrostichal setulae. Anterior scutellar setae in line with dorsocentrals. Length of lateral prescutellar setae only about twice that of acrostichals. Prothoracic coxa with 4–5 heavy setae and numerous fine ones on medial surface. Sixteen straight, sharp spines in lateral row on male prothoracic femur and about 23 longer ones of similar shape in medial row. Fourteen evenly spaced finer setae on lateral margin of ventral pollinosity. Hind tibiae dark brown, other parts of legs, including femora, lighter and unicolorous with pleura and notum. Wing measurements: C.I. = 0.96 (10♂♂), 1.14 (2♀♀); 4-V index = 2.55 (10♂♂, 2♀♀); 4-C index = 1.80 (10♂♂, 2♀♀). Other measurements: HW/ThL = 0.83 (9♂♂, 2♀♀).

Oviscape and spermathecae very similar to those of *C. diatropa* and not figured. Gonopods and distiphallus variable. Cercus rounded in profile, surstylus with 8–9 prensisetae, ventral epandrial lobe invariant and with short ventral setae projecting ventrad (their lengths about equal to lobe width) but gradually longer proximad. Dorsal portion of aedeagus connecting distiphallus to epandrium loose and membranous. Apex of distiphallus membranous, apparently eversible: internal sac visible in specimens with an elongate aedeagus, in specimens where apical microtrichia unapparent, aedeagus also appearing uneverted. When uneverted, distiphallus not curved strongly dorsad as figured. Gonopods always with 2 strong, scale-like, lateral setae and 2 thinner ones on dorsal margin. Variable vestiture, primarily on dorsal margin of gonopod and sometimes reduced to just 8 or 9 microtrichia. Paraphysis a small lobe on medial surface of gonopod with 3 slightly curved, sharp sensilla. Hypandrium short, ventral margin slightly cleft or uncleft. Aedeagal apodeme triangular and high laterally, apex bearing lateral flanges.

Holotype. ♂, Tukeit, British Guyana, 20.VII.1911. Back of label has written on it "L.4.b." (AMNH).

Paratypes. 9♂♂, 1♀, all with same data as holotype.

Etymology. Latin, "from Guyana," in regard to the type locality.

Chymomyza albitarsis (Hendel, 1917)

Fig. 7

Zygodrosophila albitarsis Hendel, 1917:43. Holotype, ♂, PARAGUAY: Fichbrig, S. Bernardino. (NHMW).

Zygodrosophila albitarsis Hendel, 1917; Duda, 1927:69. (Discussed probable synonymy with *Chymomyza.*)

Chymomyza albitarsis (Hendel), 1917; Wheeler, 1981:33. (Synonymized *Zygodrosophila* with *Chymomyza* in world catalogue.)

Description. This description and the one by Hendel are based only on the type, the only specimen known for the species. Hendel's description of the head is needed since the head of the type specimen has been lost. Extracted from his description: head diagonally broadened, as in *Zygothrica,* 3 orbital bristles present, the uppermost one [the posterior reclinate seta] in the middle of the head and not curved above.

The foremost bristle [the anterior reclinate] lies beside the antennae. Bristles that are medially based [the inner verticals] are largest and also pointed forwards and inwardly.

The specimen is in a bad state owing also to the dense fungal mycelia covering the body. Thorax with 8 rows acrostichal setulae, light amber. One postpronotal seta. Prothoracic coxa with 5 strong bristles and numerous finer ones. Thirteen to 14 fine, straight spines in medial row on prothoracic femur, ventral row obscured. Wing measurement: C.I. = 1.34.

Terminalia most similar to *C. microdiopsis* and *C. jamaicensis.* Like these other 2 species, cercus apically pointed, ventral epandrial lobe bearing numerous short setae along length (especially apical-medial portion), ventral margin of hypandrium strongly cleft, and ventral knob present about ½ distance along length of endophallal shaft. The species seems most closely related to *C. jamaicensis* because both possess a row of evenly spaced, short, fine setae on the flat ventral margin of the cercus. Unlike the geographically distant *C. jamaicensis,* though, aedeagal apodeme flared laterally, the ventral epandrial lobes distinctly knobbed, and distiphallus is quadrate and apically truncate. No vestiture on distiphallus and it possesses no ventral serrations.

Comments. I place this species in the *guyanensis-diatropa* lineage of the species-group due to the synapomorphies it possesses with *C. jamaicensis* as discussed above and, by judging from Hendel's description, because its head is probably modified in a manner similar to those of *C. jamaicensis* and *C. diatropa.*

IV. Phylogenetic relationships.

Although some species in the group are distinctive, patterns of genealogical relationships have not been easily discerned. Only 7 of the 43 synapomorphies were not in conflict with each other, which means that about 80% of the morphological characters are similar as a result of homoplasy (Fig. 16). Although this may be a consequence of the strict use of parsimony (and, particularly, its application to rapidly evolving characters such as those in the terminalia), I believe that this result is more a reflection that relationships among species in the group are truly obscure. Perhaps the time of species origins coincided so closely as to make the relationships among extant forms an essentially polychotomous one. Okada (1976) used a Mean-Cluster-Distance (MCD) proximity analysis and UPGA cluster analysis of a matrix of binary character states coded as either advanced or plesiomorphic. He did not indicate how the character polarities were decided, but it is interesting that he found 6 members in the *C. aldrichii* species-group to have relationships the least resolved among those in the 5 species-groups of *Chymomyza.* His analysis found the following pairs to be close relatives, but there were no apparent relationships among the 3 pairs: *C. aldrichii-C. coxata* Wheeler (the latter I have examined, and it appears to have a number of synapomorphies with several groups—my inclination is to agree with Wheeler [1952] in that its placement is uncertain), *C. mesopecta-C. procnemoides,* and *C. bicoloripes-C. laevilimbata. Chymomyza mesopecta* and *C. laevilimbata,* the 2 species not examined in this study, then, may be derived members of the large *diatropa-guyanensis* lineage, and they are not known to have broad-headed males. My analysis delineated 2 main lineages: the *mycopelates* and the *diatropa-guyanensis* lineages.

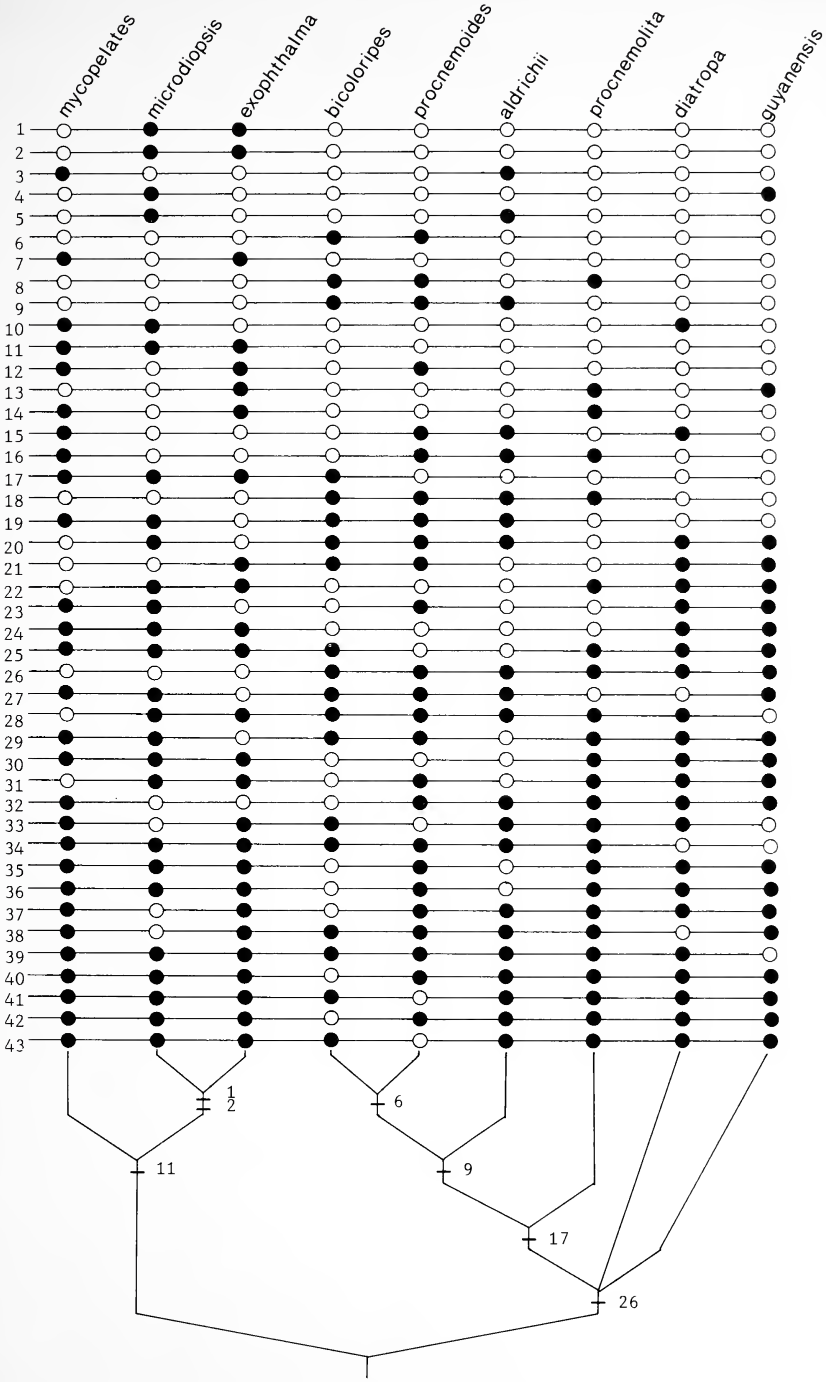

Fig. 16. Cladogram of *Chymomyza* species-group (see Table 1).

Table 1. Hypothesis of phylogenetic relationships for the *Chymomyza aldrichii* species-group (missing are *C. laevilimbata, C. mesopecta, C. albitarsis,* and *C. jamaicensis*: their affinities are discussed in the text). Apomorphies = "A," black dots on cladogram; Plesiomorphies = "P," circles on cladogram. The simplest hypothesis is provided by the branching diagram at the base of the character-state distribution matrix.

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1. Interorbital width (A = broad; P = narrow).
2. Proclinate seta position (A = equidistant between reclinates; P = closer to anterior reclinate).
3. Pleura color (A = darkened brown; P = light, thorax ground color).
4. Postalar seta length (A = shorter or equal in length to supralar; P = longer than supralar).
5. Male femoral spine length (A = undifferentiated between rows; P = lengths differ between rows).
6. Gonopod setae (A = undifferentiated; P = some are scale-like).
7. Spermathecal exterior (A = apex indented into introvert apex; P = apex smooth).
8. Procoxal seta number (A = less than 4; P = 6 or more).
9. Paraphysis seta number (A = more than 3; P = 2 or less).
10. Ventral margin of hypandrium (A = cleft; P = uncleft, margin even).
11. Eye pilosity (A = bare; P = developed).
12. Proclinate seta inclination (A = end is distant from middle of pedicel; P = ends at middle of pedicel).
13. Distiphallus vestiture (A = setose; P = glabrous).
14. Lateral aspect of distiphallus (A = pointed knob well developed; P = smooth lateral surface).
15. Facial coloration (A = dark brown area on anterior facial margin; P = unicolorous yellow or orange).
16. Spermathecal shape (A = length greater than width; P = length about equal to width).
17. Acrostichal row number (A = less than 8; P = 8 rows present).
18. Ventral margin of endophallal shaft (A = smooth, projections lost; P = projection developed).
19. Gonopod apex vestiture (A = microtrichia lost; P = microtrichia developed).
20. Ventral epandrial lobe seta lengths (A = undifferentiated; P = differentiated).
21. Lateral prescutellar seta length (A = 2× acrostichal setula length or less; P = greater than 2× acrostichal length).
22. Gonopod seta number (A = more than 1 scale-like seta; P = 0 or 1).
23. Paraphysis (A = rudimentary, inconspicuous; P = prominent).
24. Dorsocentral seta positions (A = in line with anterior scutellars; P = lateral to line extending from anterior scutellars).
25. Costal index (A = less than 1.20; P = greater than 1.40).
26. Apical ventral epandrial lobe setae (A = few, long; P = numerous, short).
27. Gonopod shape (A = pointed; P = rounded).
28. Notopleural seta lengths (A = differentiated; P = same).
29. Subvibrissal seta lengths (A = differentiated; P = homomorphic).
30. Minute orbital seta between proclinate and posterior reclinate setae (A = lost; P = developed).
31. Spermatheca size (A = small, 100 μm diam. or less; P = 150 μm or more).
32. Prensisetae number (A = reduced, less than 10; P = 11 or more).
33. Lengths of ventral epandrial lobe setae (A = long, more than 2× lobe width; P = short, length about = to lobe width or shorter).
34. Lunule coloration (A = bright yellow; P = head ground color).
35. Dorsal margin of epandrium (A = short, ½ ventral length or less; P = long, about ¾ length of ventral portion).

Table 1. Continued.

36. 4-C index (A = greater than 1.40; P = 1.40 or less).
37. Lateral profile of male cercus (A = rounded; P = pointed).
38. Distiphallus base (A = profile even; P = serrations developed).
39. Male prothoracic femoral spine numbers (A = reduced, 15 or less in either row; P = numerous, 16 or more in either row).
40. Paravertical seta sizes (A = short, less than 2× length postocellars; P = 2× postocellar length or greater).
41. Distiphallus shape (A = rounded in profile; P = pointed or sharp).
42. Vein dm-cu coloration (A = surrounding area hyaline; P = infuscated).
43. Costal cell and adjacent regions (A = infuscated dark brown; P = no infuscation).

The former is based on the possession of glabrous eyes and the latter by the presence of a few, long apical setae on the ventral epandrial lobe of the male terminalia.

DISCUSSION

I. Neotropical diversity.

Thirteen of the 16 species of neotropical *Chymomyza* are members of the *C. aldrichii* species-group. The species-group is restricted to the New World and has 2 relatively derived nearctic members (*C. aldrichii* and *C. procnemoides*). It appears from my work that the *Chymomyza* fauna of Central and South America is probably twice that presently described. For this reason, and because of the paucity of specimens from different localities, the historical biogeography of *aldrichii* group species within the Neotropical Region must be left for future work. It does appear, however, that the group may have an African origin. According to Okada (1976), the *procnemis* species-group is the sister taxon to the *aldrichii* group. Of the 11 species in the former group (Okada, 1981; Wheeler, 1981), there is a polychotomous clade among them, all of them being derived species, and they include 4 African (primarily Ivory Coast) plus the New World species, *C. procnemis* (Williston). Distributions of most of the remaining, primitive species (sensu Okada, 1976) in that group are southeast Asian (India, Java, New Guinea, Philippines, Sumatra). Dating of an Africa-South America vicariance event would place the origin of the New World *aldrichii* radiation at about 75 million years ago, or in the late Cretaceous (Dott and Batten, 1971).

The other neotropical *Chymomyza* that are members of groups other than the *C. aldrichii* species-group are *C. mexicana* Wheeler (in the *C. costata* species-group) and, in the *procnemis* species-group, *C. pectinifemur* Duda and *C. procnemis*. *Chymomyza mexicana* is distinguished by its black body color, including the fore tarsi, and the latter 2 possess milky-white apical wing spots and a light body color similar to that of most *C. aldrichii* group members.

II. Breeding and feeding sites.

Chymomyza aldrichii species-group members are associated with wood, particularly injured and decaying portions. This is in strong contrast at least to the polyphagous species *Chymomyza amoena,* a common nearctic fly whose breeding sites have been relatively well surveyed. As adults, the *C. aldrichii* group flies feed on either the tree sap or a combination of this plus the bacteria, yeasts, and fungal hyphae and spores occurring in it that cause its natural decay. It is unclear on what portions of injured and decaying wood the larvae would feed, although, it can be assumed they use substrates similar to, but more restricted than, those used by adults.

These conclusions are based on several dozen specimens in the USNM that were found with labels referring to their food habits, plus some anecdotal notes both published and unpublished. In Washington state, 6 male *C. aldrichii* and a female were taken from a Douglas fir bolt (*Pseudotsuga menziesii*: Pinaceae) infested by *Trypodendron* and *Gnatotrichus,* and 2 more males and a female reared from the "galleries of *Trypodendron lineatum.*" In Colorado, 4 male *C. aldrichii* and a female were reared from *Picea engelmanni* (Pinaceae), and 4 males and 3 females were captured on aspen (probably *Populus*: Salicaceae) trunk wounds. A single male of this species was taken in Idaho from *Pseudotsuga menziesii* (Pinaceae). Wheeler (1952) mentioned that numerous *C. aldrichii* in the collection at the University of Texas from the western United States were caught over peeled areas on the bark of aspen (*Populus*), fir (*Abies*) and Pine (*Pinus*), and the larvae of some from Minnesota were found in the bark of *Populus grandidentata* and *P. tremuloides.* Decaying logs of *Pinus alba* and *Populus tremuloides* are also mentioned as hosts, with *Betula alba* (Betulaceae) bark, by Teskey (1976). A female of *C. procnemoides* was taken in Virginia on "Tulip-poplar sap" (probably that of *Liriodendron*: Magnoliaceae).

The neotropical members of the group are likewise associates of trees, but as far as known only as adults. A male of *C. bicoloripes* in the USNM collection bears a label "on rubber [*Hevea brasiliensis*: Euphorbiaceae] tapping panel." This is supposedly one habit of *C. bicoloripes* in Costa Rica (Carpenter, 1954). The species to which Carpenter's account actually refers, though, is probably *C. mycopelates*: In the same collection is a large series of males and females, all of them captured in Costa Rica on *Ceratostomella* fungus (Conidiophoraceae) that was infesting the latex tapping panels of rubber trees. According to Carpenter's record, the flies not only passed up visiting nearby infructescences of *Fusarium* (Myxomycetes), but their attraction to *Ceratostomella* is probably a result of an odor produced by a specific combination of amyl acetate and butyl alcohol that is distinctive to the group of fungi to which this genus belongs. Five males in the USNM of *C. diatropa* were similarly caught in Costa Rica. In addition, the specimens of *C. exophthalma* that I collected in Peru were swept over cut logs and sawdust of a tree (family Lecythidaceae) in a tropical-moist inundation forest (Rio Tambopata Reserve, Madre de Dios). Unlike most other drosophilids in the area, these flies were not found by sweeping understory vegetation, or over macrofungal sporophores and fallen fruits and flowers. Broadhead (1984) discussed morphological traits associated with fungal grazing by adult Lauxaniidae. Although these *Chymomyza* show no obvious pseudotracheal modifications (i.e., prestomal teeth) nor an enlarged labella, as in most mycophagous lauxaniids, a gut content analysis would provide useful information as to the actual foodstuff.

The association of *C. aldrichii* group flies with certain woody tissues of trees is probably a specialization derived from a primitive polyphagous habit. *Chymomyza amoena,* for example, has been reared from various decaying fruits and plants such as *Symplocarpus* (Araceae) spathes and broomrape (*Conopholis*: Orobanchaceae) in New York and from apples, pears, and crabapples (*Pyrus coronaria*: Malvaceae) in Michigan. It appears especially fond of walnut and butternut (*Juglans*: Juglandaceae) husks throughout much of its range, which are no doubt its natural hosts. Outgroup comparison, then, shows that there is also a predilection for woody, fibrous, and decaying plant tissues in several plant taxa. The only mention of larval morphology in the group is a habitus drawing of *Chymomyza aldrichii* by Teskey (1976, 1981).

III. Sexual dimorphism and behavior.

A. Head shape analysis: Interspecific comparisons.

Five ratios of 6 head measurements were calculated to determine the parts of the cranium involved in male head broadening among some of the species. The ratios, denoted also by their abbreviations in parentheses, were the following: total head width/total thorax length (distance from the anterior margin of the notum to the posterior apex of the scutellum) (HW/ThL), eye depth/head depth (ED/HD), total width of eyes/head width (EW×2/HW), frontal vitta width/head width (FVW/HW), and frontal vitta width/minimum interocular distance on the face (FVW/MID) (see Fig. 17 for the location of some of these structures). Also, log-transformed values of individual male head widths were plotted on log-transformed values of their thorax lengths (a convenient and accurate estimate of body size) for males of 8 species in order to determine the linear fit of head expansion as a function of overall body size.

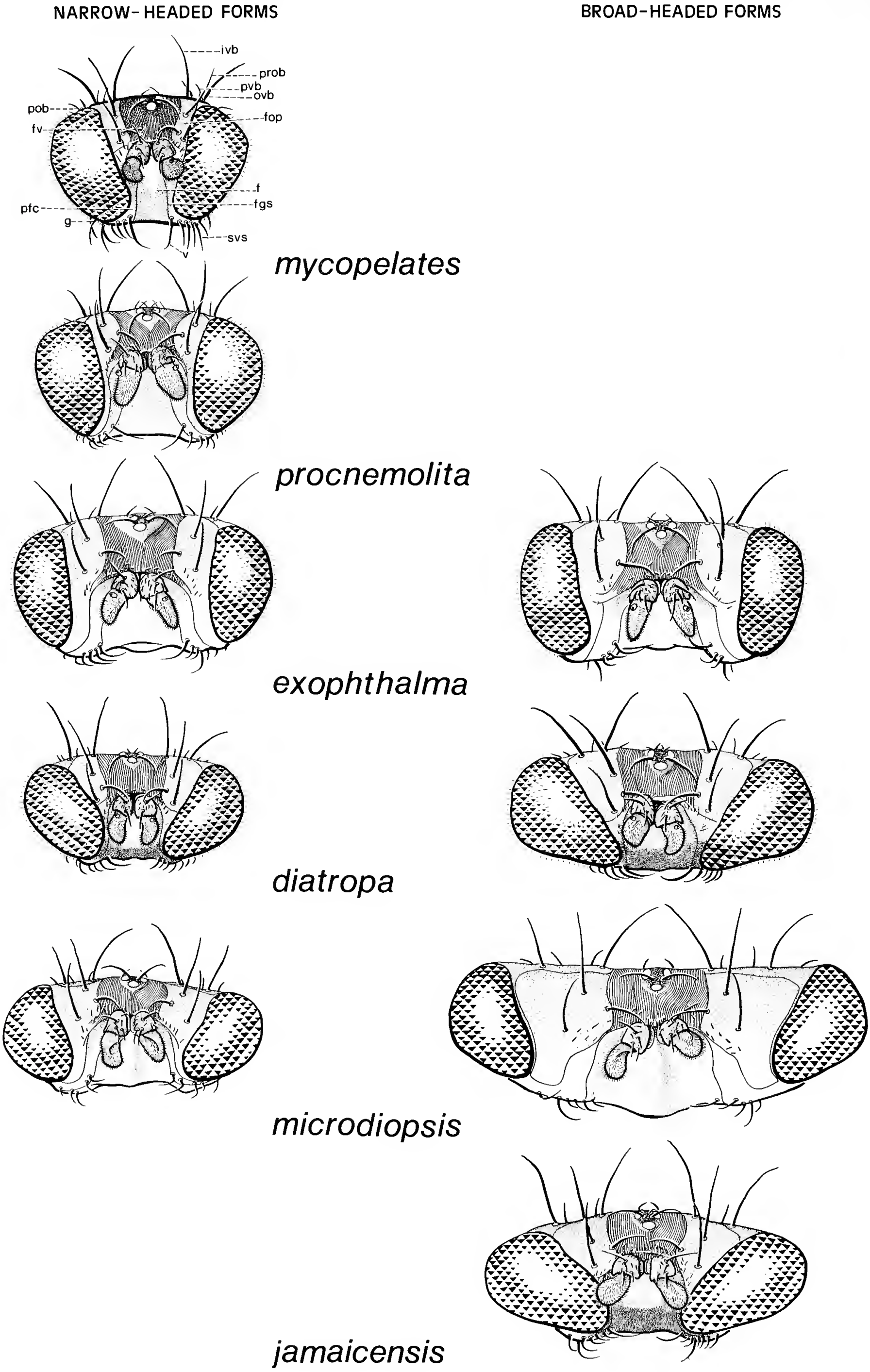
1. Relative head widths.

For 8 species where enough male specimens could be measured, all had high, positive relationships between size and head width. How much the head width varied with respect to size, though, differed considerably among species. The slope of this relationship was steepest for *C. microdiopsis, C. diatropa, C. exophthalma,* and, curiously enough, for the narrow-headed species *C. procnemolita.* Among these species dramatic differences were found in relative head widths that were not accountable just to differences in size (Figs. 17, 18). *Chymomyza amoena, C. procnemoides, C. aldrichii,* and *C. guyanensis* head sizes differ less dramatically among differently-sized males. Table 2 provides a summary of the relationships for this allometric trait.

Chymomyza microdiopsis, C. diatropa, and *C. exophthalma* have the most pronounced sexual dimorphism for the trait, the males having relative head widths (HW/ThL) 1.39, 1.12, and 1.18 times that of the females, respectively. Males of the other species have heads 0.99–1.09 times that of the relative female (mean = 0.82) head width. Also, females of the broad-headed species have slightly broader heads than the females of normal-headed species.

2. The components of the broadened crania.

Except for *C. microdiopsis,* eye depth in relation to total head depth does not vary much among species (0.80–0.91), with *C. microdiopsis* having the shallowest eyes, and the remaining species varying from 0.87–0.91 for this trait. Little or no sexual dimorphism for this trait was found.


NARROW-HEADED FORMS
BROAD-HEADED FORMS
ivb
prob
pvb
ovb
pob
fop
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g
svs
v
mycopelates
procnemolita
exophthalma
diatropa
microdiopsis
jamaicensis

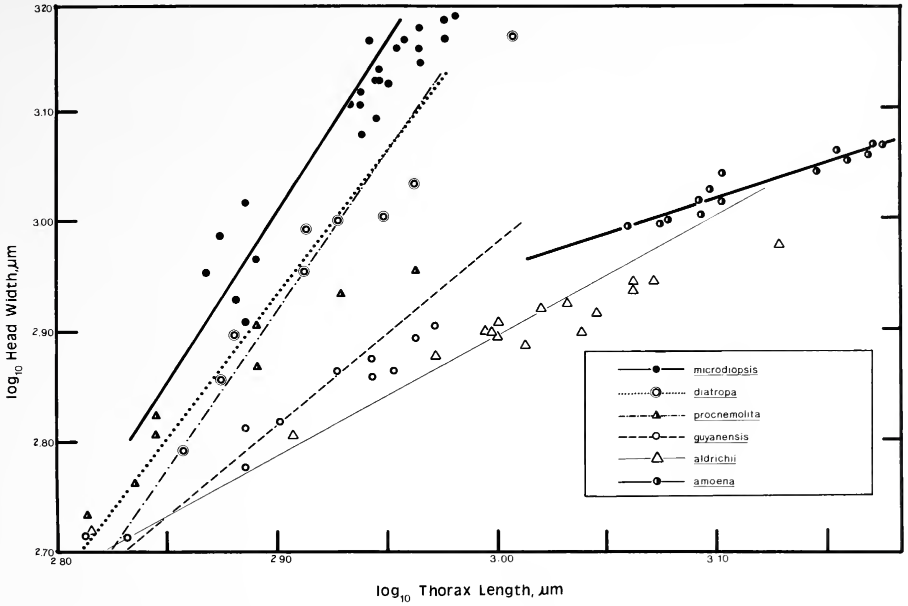

Fig. 18. Allometric relationships for male head widths as a function of body size (thorax length) for 6 *Chymomyza* species. Linear regression equations of the log-log plots are presented in Table 2.

Eye width varies considerably in relation to total head width among species. Two species having very narrow eyes, *C. microdiopsis* (EW×2/HW = 0.51) and *C. exophthalma* (0.46), are also species with extreme-type males. The mean and range of values for this trait for other species is 0.75 (0.64–0.79). Females of *C. microdiopsis* (0.68) and *C. exophthalma* (0.64) also have significantly narrower eyes in relation to their head widths compared to other *Chymomyza* females (mean = 0.75, range = 0.71–0.84).

Since, in *C. microdiopsis* and *C. exophthalma* males, the relative frontal vitta width (FVW/HW) is not expanded, their broad heads are due to a lateral expansion of the fronto-orbital and parafacial plates (Fig. 17). Females of these species share the trait, but in them it is much less pronounced. FVW/HW varies from 0.26–0.44 for males and females with no obvious sexual dimorphism. The relation between eye separation and the role of cranial sclerites causing it can be seen even more dramatically as the

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Fig. 17. Frontal view of some male *Chymomyza* heads, all to the same scale. Broad-headed forms (in the right column) and the narrow-headed form are shown for some species and were chosen to represent the range in the morphocline; for those species represented by only one form either the variation for head shape is unknown (*C. jamaicensis*) or insignificant. Abbreviations: f, face; fgs, fronto-genal suture; fop, fronto-orbital plate; fv, frontal vitta; g, gena; ivb, inner vertical bristle (seta); ovb, outer vertical seta; pfc, parafacial plate; pob, post-orbital seta; prob, posterior reclinate seta; pvb, post-vertical seta; svs, subvibrissal seta; v, vibrissa.

Table 2. Log_{10}-log_{10} linear regressions of male *Chymomyza* head widths (μm) as a function of total thorax lengths (μm).

Species	Relation y = mx + b	r^2	N
**aldrichii*	0.76x + 0.61	0.90	16
**microdiopsis*	2.00x − 2.78	0.81	24
**diatropa*	1.22x − 0.61	0.32	9
**guyanensis*	1.06x + 0.26	0.92	9
**procnemolita*	1.48x + 1.40	0.94	11
exophthalma	1.73x − 2.12	0.74	5
procnemoides	0.63x + 1.20	0.77	9
**amoena*	0.61x + 1.13	0.90	14

* Relationships are plotted in Figure 18.

ratio of FVW/MID, where this value is smallest for *C. exophthalma* (0.57) and *C. microdiopsis* (0.53), but averages 1.30 (1.11–1.50) for males of the other species. It is interesting that, even though the males have distended eyes, *C. diatropa* and *C. jamaicensis* still retain a relative interocular distance (MID/HW) about equal to that of "normal" species. These 2 species have, however, a lateral expansion of the fronto-orbital plates on the dorsal part of the head and the parafacial plates remain of normal size.

In conclusion, for species with males that are conspicuously broad-headed, either the absolute eye size has remained unchanged in comparison to close relatives (i.e., *C. exophthalma–C. microdiopsis*) or it has been enlarged by a lateral extension of each eye. Either the parafacial plates, or the eyes, but not both, and always the fronto-orbital plates have become laterally distended in the highly modified males. Females of the species having broad-headed males share the trait but for them it is much less pronounced. This suggests that bizarre, sexual modifications of *Chymomyza* heads (and probably those of some other Acalyptratae) are dramatic accents to modifications that have occurred first in both sexes.

3. Phylogenetic considerations of broadened crania.

Because the females of *C. jamaicensis* and *C. albitarsis* are unknown, these species were not included in the cladogram in Figure 16. Based solely on the males, however, they seem closely related to *C. diatropa* since at least *C. jamaicensis* and *C. diatropa* have conspicuously darkened anterior facial margins and because the eyes are distended in the same manner for all 3 species. Were this the case, then the evolution of broad-headed males would have taken place at least twice in the *C. aldrichii* species-group: Once in the *diatropa-guyanensis* lineage, where males have expanded eyes, and again in the *mycopelates* lineage, where the modification is a result of the involvement of 2 sets of frontal sclerites. Other drosophilid genera with members having broad-headed males reflect the 2 modes by which *Chymomyza* heads have broadened. *Drosophila heteroneura* (Perkins), a Hawaiian species, has normal eyes lying on expanded fronto-orbital and parafacial plates (the facial plate, too, has been expanded). Five species of *Zygothrica* (Wiedemann), on the other hand, have males whose eyes are distended very much like those of *C. jamaicensis* and *C. diatropa* but in some of these species the modifications are much more extreme. It is interesting that one broad-headed member of each of the 2 lineages is probably a Caribbean island endemic: *C. microdiopsis* on Cuba and *C. jamaicensis* on Jamaica.

B. Leg ornamentation and reproductive behavior.

Spines, which are found only on the males of most *Chymomyza* species, are derived from the finer setae distributed evenly over the leg integument. This is based on the observation that both types of integumental outgrowths have a socketed base and possess longitudinal striae (Fig. 15). Ventral to the spines is fine pollinosity (Fig. 15), which is derived from the microtrichia also distributed evenly over most of the cuticle but, here, it is in dense patches and stands erect. The spines can vary in number per row (7–21), thickness, length, shape (Fig. 15), and their location. *Chymomyza mesopecta,* for instance, has lost the profemoral spines and instead developed them on the mesothoracic femora in males. The spines always occur in 2 rows.

Other than the loss of profemoral spines in the males of *C. bicoloripes* and *C. mesopecta,* synapomorphies for the character complex are few. Even closely related species can differ greatly in spine morphology: *C. diatropa* has 8 medial and 10 ventral, long spines and *C. guyanensis* has 23 medial and about 16 ventral, somewhat shorter spines (Fig. 15). Male femoral spines must evolve, like the terminalia and heads, at rates much faster than the rest of the phenotype. Although the spines no doubt function in male courtship and/or mating, they are probably ineffectual during intermale aggression. This conclusion is based on some behavioral observations, as well as the fact that no patterns of spine development occur concomitant with changes in head shape, the latter being a trait well known in some Diptera where head-butting contests among males take place.

Several individuals of *Chymomyza exophthalma* were kept in glass culture vials on instant drosophila medium (Carolina Biological Supply Co.) on 10, 11 October 1984, in Tambopata, Peru, and their behavior was observed. Like most *Chymomyza,* especially for the males, individuals were found to move quickly about in rapid stop-and-turn motions reminiscent of phorids. The sprints extended for about 5–10 body lengths. Periodically while sprinting, and sometimes immediately upon stopping or just before turning, the forelegs were extended laterally to about 3 times the width of the body. This was done either as a single motion to 3 times consecutively, and was usually repeated rapidly (once every 5 to 10 seconds). Generally every time the legs were extended, the wings were simultaneously spread from between 90° to usually closer to 180° apart from each other. In unison, these motions gave the fly the appearance of swimming. Also, as the fly stopped to turn, it usually would "paw" the ground with 3–4 alternate strokes of the forelegs, then either "swam" or walked on.

During confrontations, which lasted between 4 and 16 seconds (7 observations), a pair would meet head-on and about ½ a body length apart. The meso- and metathoracic legs remained planted but the prothoracic legs were raised so that the tarsi were above the dorsal surface of the body. The legs were then lashed out against the opponents' tarsi (and perhaps other parts, such as the face) and, if the "standoff" escalated, each fly gradually raised itself higher from the substrate but to no more than twice the original stance height. Just prior to the "standoff" there often were

2–3 very rapid wing scissors, and during the "standoff" the wings were briefly outstretched about 100°. Male-to-male and male-to-female confrontations were similar, except that females did not scissor their wings. Flies never seemed to approach each other close enough so as to contact each others' femoral spines during encounters, although they might have been able to detect them at least given the way they were exposed to the opponents. I observed no males butting heads, but more extended observation would likely prove more fruitful. Also, no courtship or mating was observed.

ACKNOWLEDGMENTS

Field work in Peru was funded by a research fellowship from the Harold E. Moore Fund of the Cornell University Bailey Hortorium. I was also able to peruse the USNM collection with the aid of a Smithsonian Short-term Visiting Fellowship. The Division of Biological Sciences at Cornell allotted me use of an SEM, and general services were provided by Hatch grant #NY(C)-139426 to Quentin D. Wheeler. Ruth Contreras-Lichtenberg made available to me a loan of Hendel's type specimens: to her and the others previously mentioned I extend my gratitude. E. R. Hoebeke, J. Frank McAlpine, Wayne Mathis, and Stephen Nichols provided useful suggestions on the original manuscript. It is my pleasure to dedicate this work to Drs. Hans Burla and Hampton Carson, to honor them on their retirements.

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Received March 26, 1985; accepted July 29, 1985.

J. New York Entomol. Soc. 94(3):372–376, 1986

A NEW *DROSOPHILA (HIRTODROSOPHILA)* FROM MALAYSIA WITH BROAD-HEADED MALES (DIPTERA: DROSOPHILIDAE)

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Abstract.—Drosophila caputudis, new species, from Kuala Lumpur, Malaysia is described and figured. It is the only *Hirtodrosophila* known to have males with heads that are laterally distended.

After completing a revision on South American *Chymomyza,* I received specimens of *Drosophila* with a sexual dimorphism similar to that of some of the *Chymomyza.* This extends our knowledge of the repeated arisal of broad-headed male Drosophilidae, and the trait is now known in *Drosophila* (*Idiomyia*) *heteroneura* (Perkins) [endemic to Hawaii], several described and undescribed *Zygothrica* [all of them neotropical (Burla, 1954; Grimaldi, unpublished)], 5 neotropical species of *Chymomyza* (Grimaldi, 1986), and in the southeast Asian species *Lissocephala asiatica* Okada. The last was transferred to *Zygothrica* when the bizarre males were discovered (Okada, 1965), but has since been returned to *Lissocephala* (Okada, in manuscript and personal communication) since closer examination shows its affinities to be quite distant from *Zygothrica* and to truly lie with some southeast Asian forms. A forthcoming paper of mine will treat the occurrence, anatomy, allometry, and functional consequences of the trait in Drosophilidae.

Hirtodrosophila is presently considered as a subgenus in the huge (and paraphyletic) genus *Drosophila.* Burla (1957) provided the most thorough exposé on *Hirtodrosophila,* but for South American forms in particular. Duda (1923, 1924) was the first to deal in depth with those from southeast Asia, then Okada (1967) and Bächli (1973). Okada divided the Old World species into three groups and some of these again into subgroups.

Drosophila (Hirtodrosophila) caputudis, new species
Figs. 1, 3

Description. Male head with expanded fronto-orbital plates (head width/thorax length = 1.25, 6♂♂). Eyes rosy pink; interfacetal setulae short but dense apically. Anterior reclinate seta anterior to proclinate by less than its length, lateral to proclinate by about equal to its length. Postocellars cruciate. Inner verticals subparallel, outer verticals divergent; 1–2 very long postverticals. Ocellars slightly divergent. Cranial setae lengths (longest to shortest): inner verticals-posterior reclinates-outer verticals-ocellars/postocellars-proclinates-anterior reclinates. Vibrissa very fine, length about that of proclinates, projecting anterodorsad, subtended by about 5 very fine setae. Prominent, long thin genal seta per side. Ocelli light, contrasting with dark brown

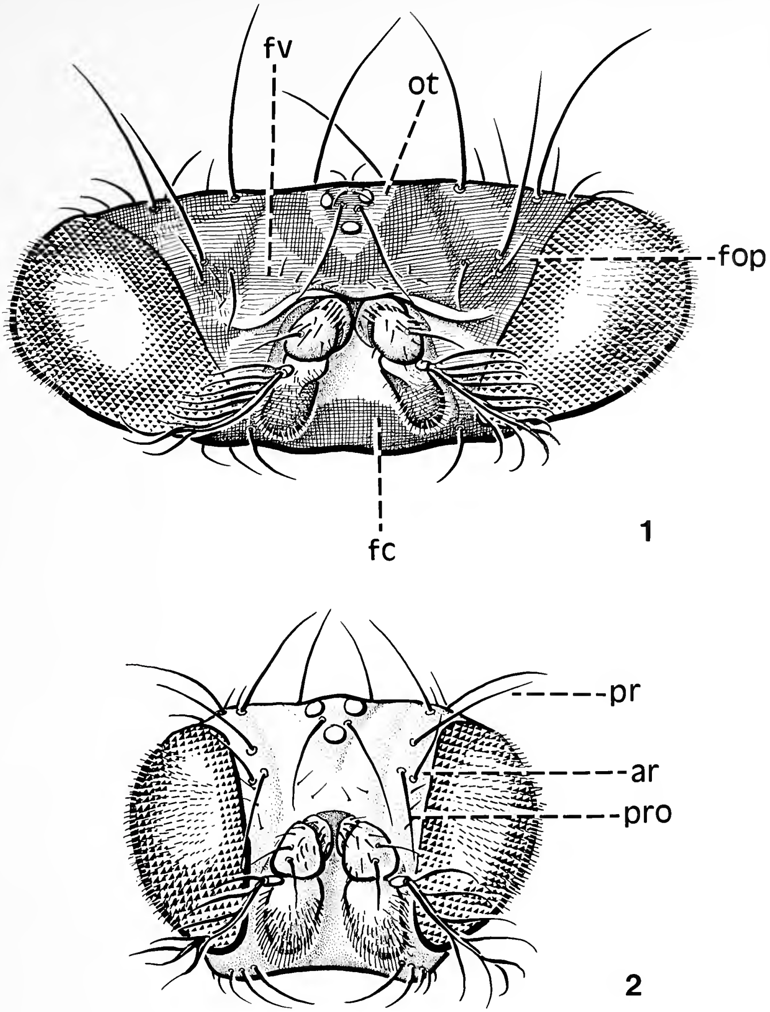

Fig. 1, 2. 1. Male *Drosophila* (Hirtodrosophila) *caputudis,* n. sp. Frontal view of head. fc, face; fop, fronto-orbital plate; fv, frontal vitta; ot, ocellar triangle. 2. Male *Drosophila* (Hirtodrosophila) *duncani* Sturt. (Ithaca, N.Y.) Frontal view of head. ar, anterior reclinate seta; pr, posterior reclinate orbital seta; pro, proclinate orbital seta.

ocellar triangle. Frontal vitta dark brown; brown markings circumscribing bases of orbital setae and connect to frontal vitta. Occiput with dark brown area near eyes. Scapes and lunule yellow, like flagellomeres I and II. Pedicel light to dark brown, arista dark brown. Face light yellow, no carina. Ventral margin of face with distinctive, discrete dark brown border extended dorsad to just past tips of flagellomere I. Clypeus dark brown; each palpus with 2 apical setae. Proboscis short, labellum yellow. Oral

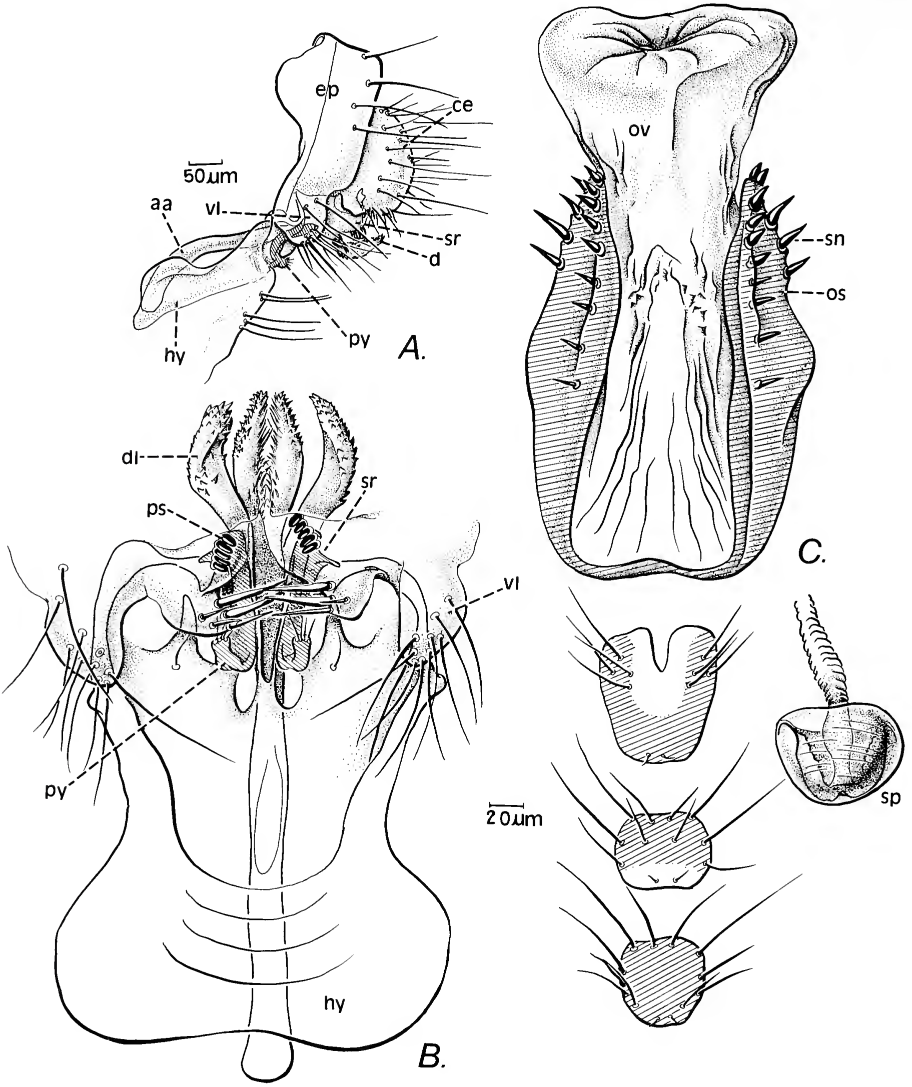

Fig. 3. a) Lateral view, male terminalia of *D. caputudis,* n. sp. aa, aedeagal apodeme; ce, cercus; d, distiphallus; dl, distiphallus, lateral lobe; ep, epandrium; hy, hypandrium; ps, prensisetae; py, paraphysis; sr, surstylus; vl, ventral lobe of epandrium. b) Male genitalia of *D. caputudis,* n. sp., ventral view. c) Female terminalia of *D. caputudis,* n. sp., ventral view. os, oviscape (=sternite VIII); ov, oviprovector; sn, sensillum; sp, spermatheca.

cavity wide. Flagellomere about twice length of pedicel. Arista with 6–7 dorsal and 1–3 (usually 2) ventral rays. Postocciput dark brown, cheeks and genae contrasting light yellow.

Mesonotum dark brown, indistinct edge extended about ⅘ width of notum. Apical ⅔ scutellum dark brown, margin light yellow. Six rows acrostichal setulae. Pleura light yellow, except for dark to light brown area at wing base. Two prominent katepisternal setae. 1 large postpronotal seta, 2 large supra-alar, 1 lateral prescutellar (length about twice that of acrostichals). Anterior scutellars parallel, posterior ones divergent, lengths equal. Posterior dorsocentral thoracic seta longest, lying ½ distance between anterior dorsocentral and scutellar suture. Subscutellum and halteres light yellow. Anepimeron and anepisternum with dark markings, but variable for this trait. Legs yellow to tan, no distinctive markings or ornamentations. Pleura mostly yellow. Wings hyaline, veins dark, very dense microtrichia on membrane.

Abdominal tergites dark brown, epandrium and cercus light yellow like lateral portions of tergites 3–6. Sterna and surrounding membrane light yellow. Tergal setae evenly arranged in 3–5 transverse rows, the posterior one with longest setae. Male terminalia with evenly rounded cercus (in profile), its ventral surface with numerous short setae. Ventral epandrial lobe small, bearing 14–16 setae; smaller medial lobe on each side with 4–5 sharp, straight setulae projecting mediad. Surstyli each with 5 short prensisetae. Anterior margin of hypandrium bilobed; length about that of aedeagal apodeme. Paraphyses small. Hypandrium with anterior lobes curved ventroapicad, each with 4 short setulae. Aedeagal apodeme bent ventrad in profile. Endophallus ornamented, with 3 lobes, median one cleft with sharp setulae and scales on inner margins and distal half of lateral margins, each lateral lobe also with some sharp scales. Oviscape (sternite VIII) with 13 sharp sensilla on each laterally-broadened surface (valve), 9 of them ventral. Membranous, eversible egg guide (oviprovector) without well-developed scales. Posterior margin of sternite 7 cleft, 2 groups of 4 setae on each side. Spermathecal capsule smooth and large, heavily sclerotized, dome-shaped, with a small apical indentation.

Holotype. ♂, MALAYSIA: Kuala Lumpur (no dates available), D. Burkhardt, I. de la Motte, colls. (in National Museum of Natural History, Washington, D.C.).

Paratypes. 9♂♂, 6♀♀, all with same label data as holotype (NMNH).

Comments. This species is in the *quadrivittata* species-subgroup of the *Drosophila* (*Hirtodrosophila*) *quadrivittata* species-group, based on Okada's (1967) phylogenetic groupings. It will key out to couplet 20 in his key, as *D. latifrontata* "var. *sublineata,*" although it shares closer relationships with other species. Subgroup placement is based on the possession of flagellomere I setulae lengths being relatively reduced, and an endophallus that has lateral lobes. It is very similar to the Japanese species *D. yakushimana* Okada, the most exceptional differences being that the new species has a flat face (no carina) and a broad head in the males, the oviscape is apically pointed and has 13 instead of 20 sensilla, and the male terminalia vary in several details. Any comments on distribution must await better collecting in southeast Asia.

Male head structure shows remarkable convergence with that of *Chymomyza jamaicensis* and *C. diatropa* (Grimaldi, 1985). All 3 species have the eyes expanded ventrally, but not dorsally, and a slightly expanded facial plate bears a distinct dark anterior margin. The fronto-orbital plate expansion accounts for most of the head broadening since the frontal vitta width (relative to thorax length) is normal in comparison to other *Drosophila.*

ACKNOWLEDGMENTS

I thank Drs. Dietrich Burkhardt and Ingrid de la Motte (University of Regensburg) who, when they learned of my interest in broad-headed Drosophilidae, sent to me the Malaysian specimens, and Dr. Toyohi Okada who provided comments on the description.

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Received March 26, 1985; accepted July 29, 1985.

J. New York Entomol. Soc. 94(3):377–382, 1986

A NEW SPECIES OF *MYOLEPTA* (DIPTERA: SYRPHIDAE) FROM NEPAL, WITH ITS PHYLOGENETIC PLACEMENT AND A KEY TO ORIENTAL SPECIES

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Abstract.—A new species, *Myolepta graciliventris* Wiegmann (Diptera: Syrphidae), is described from Nepal. A revised key to the Oriental *Myolepta* is included. Phylogenetic relationships among subgroups of the genus are reviewed.

Three species of Oriental *Myolepta* have previously been described, one from the Himalayas and two from Thailand. A new species from Nepal is described in this paper. The genus *Myolepta* is traditionally distinguished by its short antenna that are about half as long as the face with an oval third segment, spinose femora, bare metasternum, and dimorphic face (male with tubercle and female without tubercle). Assessing apomorphic character states, Thompson (1974) divided *Myolepta* into 6 groups: *scintillans* and *strigilata* groups for the New World species and *africana, petiolata, orientalis* and *luteola* groups for the Old World. The *luteola* group has retained the primitive pilose condition of the katepimeron and metasternum (Thompson, 1974). The New World groups, *scintillans* and *strigilata,* are characterized by their scale-like pile and bare metasternum, while the divergence of the Old World groups is evidenced by an elongation of the third antennal segment. Within the tribe Chrysogasterini, the presence of femoral spines on all legs is a synapomorphy uniting *Myolepta* and its sister-group *Lepidomyia* Loew (Thompson, 1972). The species of *Lepidomyia* differ from the *Myolepta* by the presence of a facial tubercle in both the male and female. The phylogenetic relationships within the genus *Myolepta* are shown in Figure 1.

While retaining Thompson's classification of the new world *Myolepta,* a revision must be made of the Old World groups with the addition of the new species, *M. graciliventris. M. himalayana* Brunetti (1923) is the only previously described *Myolepta* from the Himalayan region; its short antennae and oval third antennal segment placed it in the *luteola* group. The two species from Thailand, however, differ by having elongate antennae, as long as or longer than face, and an elongate third antennal segment (synapomorphy) (Thompson, 1974). The three Ethiopian species also possess elongate antennae. These species, the *africana* group, form the sister group to the *orientalis,* the only other Old World group with scale-like pile (Thompson, 1974). The new species, *M. graciliventris,* is easily distinguished by its only slightly constricted ventrally curved abdomen, greater than half its maximum width at its minimum, an apomorphic character with respect to the *orientalis* group. The abdomen of *petiolata* is strongly petiolate, less than half its maximum width at its minimum, while that of *orientalis* is oval. Despite its Himalayan distribution, *M. graciliventris* appears to be more closely related to the Thai species than to *M. himalayana,* as it lacks the prominent facial tubercle in the male and has elongate antennae. Consequently, *M. graciliventris* can be considered a plesiomorphic sister-group to both *africana* and *orientalis* groups due to its lack of scales, and apomorphic with respect to *petiolata* on the basis of scutellar sulcus (Fig. 1). A revised key to the Oriental *Myolepta* follows.

KEY TO THE ORIENTAL SPECIES OF *Myolepta*

1. Antennae short, less than one-half as long as face; third antennal segment oval; scutellum black (India) .... *himalayana* Brunetti (1923)
– Antennae long, about as long as or longer than face; third antennal segment elongate; scutellum not all black, with some light color 2
2. Abdomen petiolate, less than half its maximum width at its minimum; scutellum orange, without marginal sulcus (Thailand) .... *petiolata* Thompson (1971)
– Abdomen not petiolate, oval or only slightly constricted at base, greater than half its maximum width at its minimum; scutellum black with some light color, with marginal sulcus 3
3. Abdomen oval; scutellum black, with a yellow apical sulcus (Thailand) .... *orientalis* Thompson (1971)
– Abdomen slightly constricted at base of second segment, greater than half its maximum width at its minimum (Fig. 3); scutellum black with white apical sulcus (Nepal) .... *graciliventris,* new species

Myolepta graciliventris, new species
Figs. 2–6

Description. A blackish, gray pollinose fly with a slightly constricted abdomen and black scutellum with a white apical sulcus.

Holotype male. Head (Fig. 4): Face golden pollinose with short gold pile: gena and clypeus shiny dark brown and bare; anterior tentorial pit extending ¾ length to antennal base; frontal triangle golden pollinose; frontal lunule shiny, orange; vertex shiny, black, elongate; occiput white pollinose with white setae along margin, bare along eye margins. Antennae nearly as long as face, yellow except with first segment slightly darker; third segment elongate, more than twice as long as wide; first segment with three short black dorso-apical bristles; second segment with six short black dorso-apical bristles, with first apical bristle prominent; arista orange basally, dark orangish-brown apically, as long as antenna. Eye contiguity as long as ocellar triangle.

Thorax (Fig. 3): Dorsum slightly longer than broad, brownish-black, gray pollinose with short pale golden hairs: transverse suture discontinuous golden pollinose, extending ⅓ over dorsum on each side; pronotum gray pollinose, with pollinosity extending onto anterior margin of scutum; postpronotal lobe gray pollinose, except apical ¼ shiny, brownish-black and bare; postalar callus lighter brown with short golden hairs; scutellum dark brownish-black fading gradually to white apical margin, with broad apical marginal sulcus, and short golden hairs; proepisternum gray pollinose with pale golden hairs; proepimeron bare, gray pollinose; anepisternum shiny black, lightly gray pollinose with pale golden hairs on anterior ½, heavily gray pollinose with pale golden hairs on convex posterior ½; notopleuron gray pollinose with pale golden hairs; anepimeron shiny, black, lightly gray pollinose with pale golden

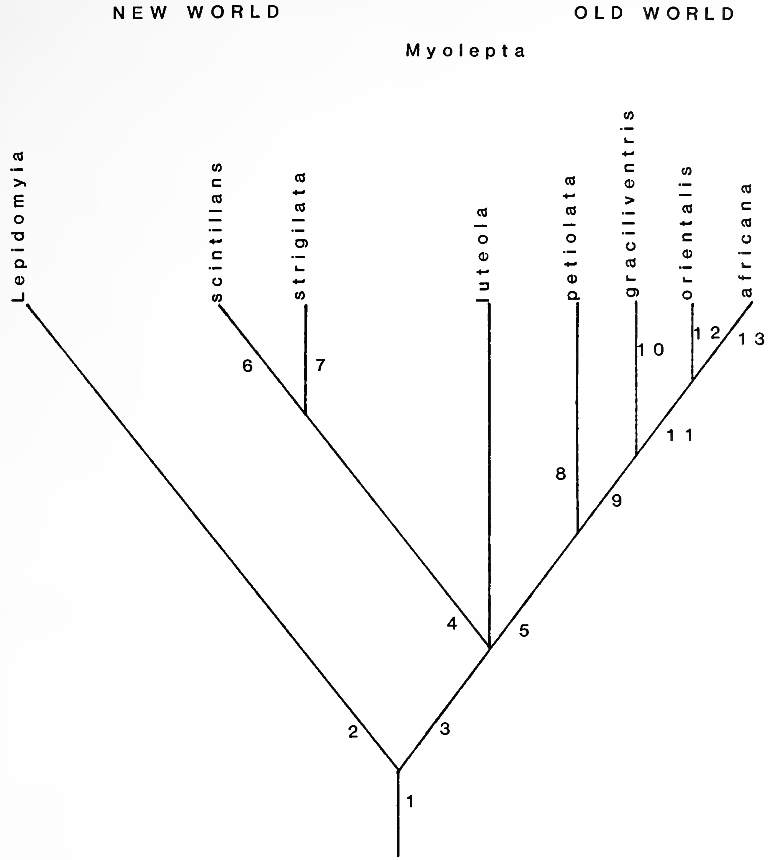
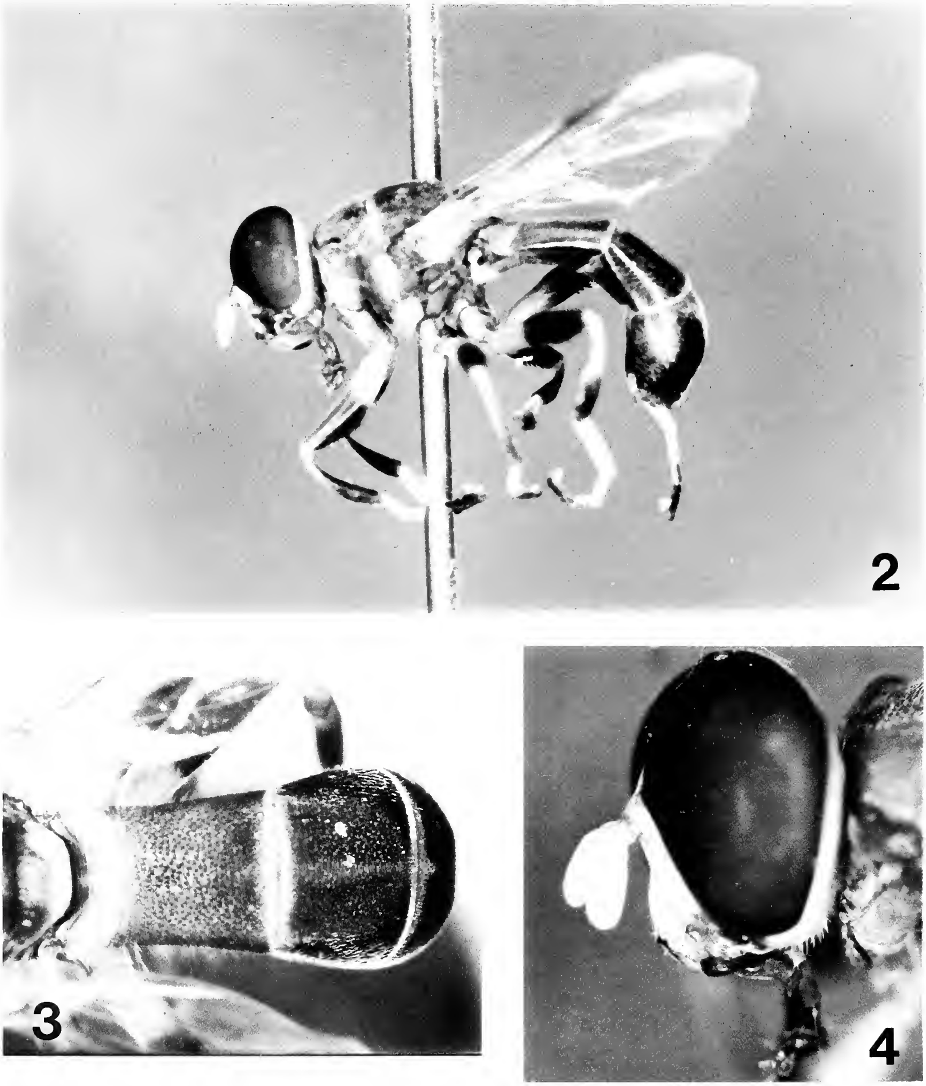


Fig. 1. Phylogeny of the genus *Myolepta* Newman. The autapomorphic character states used are: 1, femoral spines on all legs; 2, elongation of antennae, bare metasterna and presence of scale-like pile; 3, loss of facial tubercle in female; 4, bare metasterna and presence of scale-like pile; 5, elongation of third antennal segment and bare metasternum; 6, triangular scutellum; 7, bare face and cheeks; 8, petiolate abdomen; 9, broad apical scutellar sulcus; 10, slightly constricted abdomen; 11, presence of scale-like pile; 12, oval abdomen; 13, triangular scutellum.

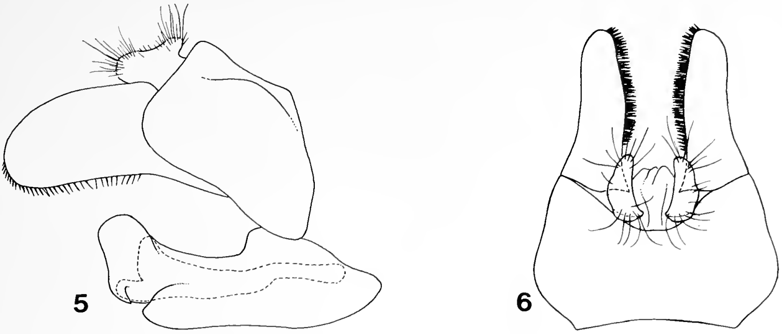
hairs; katepisternum gray pollinose with pale golden hairs on upper apical ⅓; katepimeron bare, metasternum bare, lightly gray pollinose; katatergite shiny black, gray pollinose with dense pale golden hairs; anatergite bare, lightly gray pollinose; meron shiny black, bare, lightly gray pollinose; squama white with long golden hairs on apical margin; halter yellow. Legs: coxae light brown, gray pollinose; trochanters golden; femora golden except with apical ⅓ of forefemur and midfemur and apical ½ of hindfemur dark brown on dorsal surface, with short pale golden hairs; foretibiae and midtibia golden with apical ⅓ dark brown on dorsal surface, with short pale golden hairs; hindtibia golden except with apical ½ dark brown on dorsal surface; first and second tarsomeres golden; tarsomere three on midleg golden, on foreleg and



Figs. 2–4. *Myolepta graciliventris*. 2. Habitus, lateral view. 3. Abdomen, dorsal view. 4. Head, lateral view.

hindleg brownish-black, apical two tarsomeres brownish-black dorsally; pulvilli golden. Wings: hyaline except brown apical ½ of stigma, microtrichose except entire first costal cell, all except apical ⅙ of second costal cell, first basal cell except along spurious vein, all except anteroapical ¼ of second basal cell and posterior to basal ¼ of anal cell.

Abdomen (Fig. 3): Longer than thorax, slightly constricted at base of second seg-



Figs. 5, 6. *Myolepta graciliventris* male terminalia. 5. Lateral view. 6. Dorsal view.

ment, widening posteriorly, greater than ½ its maximum width at its minimum, curved ventrally after second segment. Dorsum dark brownish-black, first segment gray pollinose, laterally brownish-black with long white hairs; second segment gray pollinose with short appressed black hairs, laterally brownish-black with long white hairs basally; apical margins of second and third terga with thin, densely golden pollinose stripe; third tergum dark brownish-black with short appressed black hairs, laterally with golden hairs; fourth tergum dark brownish-black with long appressed golden hairs and orange apical margin; genital cap brownish-black with pale golden hairs; venter black, silvery gray pollinose except fourth sternum only lightly gray pollinose with short white hairs.

Male genitalia as in Figures 5–6.

Female. Unknown.

Holotype. ♂: NEPAL, Sundarijel, 3 May 1980, Ammon Freidberg coll., (National Museum of Natural History, Washington, D.C.).

Paratype. ♂: Same data as holotype.

Diagnosis. M. graciliventris can be distinguished from the three previously described Oriental species by its abdominal shape: the petiolate abdomen of *M. petiolata* is much less than ½ its maximum width (third segment) at its minimum (second segment); the abdomen of *M. graciliventris* is only slightly constricted, or greater than ½ its maximum width (third segment) at its minimum (second segment); and the abdomen of *M. orientalis* is more ovoid than that of the new species. *M. graciliventris* can also be distinguished by the brown bands on the apical ½ of each leg segment, lack of a prominent facial tubercle in the male, broad apical scutellar sulcus, and lack of scale-like pile.

Etymology. The name *graciliventris* alludes to the slender constriction of the abdomen of the species.

ACKNOWLEDGMENTS

I thank sincerely F. Christian Thompson, Systematic Entomology Laboratory, Agricultural Research Service, Washington, D.C., for his encouragement, guidance and criticism in preparing this paper, for the loan of the specimens, and for reviewing the manuscript. In addition, I thank

Ray Gagné and an anonymous reviewer for commenting on the manuscript, Linda Lawrence for the drawings of the genitalia, M. A. Wolff for help with the cladogram, and F. E. Giles, Biology Dept., Loyola College, Baltimore, Maryland, and T. J. Kelly, Insect Reproduction Laboratory, Agricultural Research Service, Beltsville, Maryland, for their support and assistance.

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Received March 18, 1985; accepted September 17, 1985.

J. New York Entomol. Soc. 94(3):383–393, 1986

A NEW SPECIES OF THE *ANCHISIADES* GROUP OF *HERACLIDES* FROM VENEZUELA (LEPIDOPTERA: PAPILIONIDAE)

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Abstract.—Heraclides matusiki, new species, is described from a unique specimen collected in Sucre State, Venezuela, in 1912, based on an analysis of wing and genitalic characters of the *Heraclides anchisiades* species group.

With the aid of David Matusik (Field Museum of Natural History), we have been surveying incorporated and unincorporated Neotropical Papilionidae specimens at the American Museum of Natural History (AMNH) with particular emphasis on locating as yet undescribed taxa important as additions to this "well-known" butterfly group. Simultaneous with recent ecological changes influencing significant faunal extinctions in the Neotropical Realm (Brown, 1982, 1984) synoptic knowledge of terminal taxa is becoming increasingly important to current methods of systematics and biogeography. Important to this consideration is that undescribed taxa are still evident within poorly studied early collections deposited in major museums. Such depositions may represent the only extant specimens of such taxa (Rütimeyer, 1969; Johnson, Rozycki and Matusik, 1985, 1986). Initial contributions from the above-mentioned survey include recognition of the species status and previously unrecognized male of *Pterourus diaphora* (Staudinger) (Johnson, Rozycki and Matusik, 1985) and description of the little-known female of *Pterourus xanthopleura* (Godman & Salvin) (Johnson, Rozycki and Matusik, 1986). Interestingly, both of these are represented solely by specimens in European or United States museums from samples collected prior to 1920.

In 1984, among unincorporated New York Zoological Society material at the AMNH, we discovered a specimen (Fig. 1A, B) taken in 1912 at Caripito, Venezuela, which though clearly representative of the *anchisiades* Group of *Heraclides* (*sensu* Munroe, 1960; Hancock, 1983), differed notably in wing characters from any named taxon of that group. When genitalic dissection further confirmed the uniqueness of the specimen we contacted other lepidopterists studying Papilionidae as well as curators at major museums, asking their opinion of the specimen and that they search for additional examples. The breadth of response attested to the unusualness of the Caripito specimen and also emphasized the need for a taxonomic study of the *anchisiades* Group such as is presented below. Although all lepidopterists consulted agreed upon the uniqueness of the Caripito specimen, there were widely different opinions on its status and apparent affinities. Dr. Keith S. Brown (Universidade Estadual de Campinas, São Paulo, Brazil), who is preparing a synonymic list of

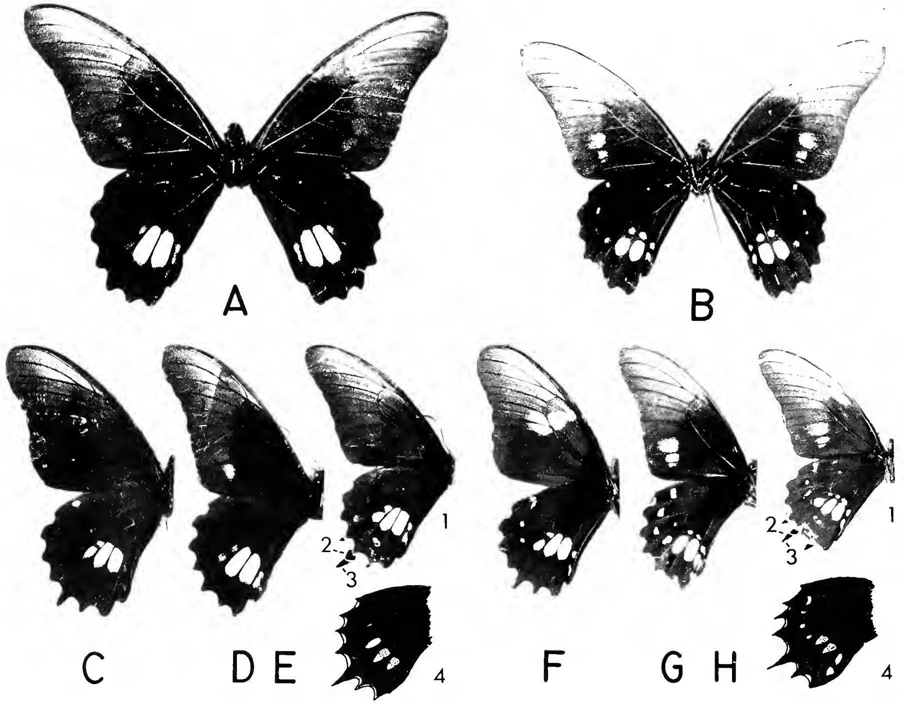

Fig. 1. Holotype *Heraclides matusiki,* A: upper surface. B: under surface. C. *H. rhodostictus pacificus* (Rothschild & Jordan), Colombia [AMNH] (upper surface) [F—under surface]. D. *H. anchisiades anchisiades,* Paramaribo, Surinam [AMNH] (upper surface) [G—under surface]. E. *H. isidorus brises,* (Rothschild & Jordan), Colombia [AMNH] (upper surface) [H—under surface]. Subscript numbers of E and H: 1—*H. i. brises*; 2—extent of terminad lengthening, vein CU_1 and adjacent veins cephalad and caudad in *H. i. isidorus*; 3—extent of same in *H. i. flavescens* (Oberthür); 4—Diagrammatic representation, maximum extent (white plus stiples) of white postmedian ellipses occurring in some Colombian and Ecuadorian *H. isidorus* and their minimum extent (stiples only) [E, upper surface; F, under surface].

Neotropical Papilionidae, viewed the specimen as a localized form of the geographically proximate congener *H. anchisiades* (Esper) (Fig. 1D). He saw the unique wing markings as either artifactual or as perhaps resulting from a localized mimicry phenomenon. He regarded the genitalic characters as simply extreme variation for the Group. Dr. Tommasso Racheli (Università Degli Studi di Roma, Rome, Italy), who is noted for his work on Neotropical *Parides* and *Battus,* saw the specimen's characters as more like those of *H. isidorus* (Doubleday) (Fig. 1E) or *H. rhodostictus* (Butler and Druce) (Fig. 1C). Dr. Lee D. Miller (Allyn Museum of Entomology, University of Florida, Sarasota, U.S.A.), who has published on various Papilionidae (particularly *Graphium*), viewed the specimen as displaying some characters traditionally used to denote all of the above species as well as the little-known *H. maroni* (Moreau), a species currently known only from a few coastal sand forest French Guianian specimens. Consequently, Miller considered the Caripito specimen as possibly representing an undescribed species. The search of four major United States museums, six major South American museums, two major European museums and three private United States collections noted for their synoptic holdings of Papilionidae yielded no further specimens like the Caripito example.

TAXONOMIC ANALYSIS

The *Heraclides anchisiades* Group (*sensu* Munroe, 1961; Hancock, 1983) includes the taxa *hyppason* (Cramer), *pelaus* (Fabricius), *oxynius* (Hübner), *epenetus* (Westwood), *chiansiades* (Westwood), *pharnaces* (Doubleday), *erostratus* (Westwood), *rogeri* (Boisduval), *anchisiades, maroni, isidorus, rhodostictus* and *erostratinus* (Vasquez). As seen in Figure 2, current usage for these *Heraclides* (Beutelspacher and Howe, 1984; D'Abrera, 1981; D'Almeida, 1965; Jordan, 1907; Munroe, 1961; Rothschild and Jordan, 1906) attributes some species level taxa of this group distinctly insular distributions (*erostratinus, rogeri, maroni*) while others are regarded as complexes of "subspecies" with wide geographic ranges (*pelaus, rhodostictus, isidorus, anchisiades*).

Table 1 reviews the major wing and genitalic characters surveyed in our study of the *anchisiades* Group. As noted by Munroe (1961), wings of these species generally are characterized by: (a) tailless South American taxa mimetic of groups of *Parides* [Papilionidae] or (b) predominantly long-tailed Central and South American taxa either non-mimetic or mimetic of tailed Triodini [Papilionidae]. Analysis of male genitalic characters of the *anchisiades* Group (Figs. 3–5), along with those of selected females, indicates structural divergence within several of the so-called "subspecies" complexes approaching and/or exceeding that within some of the presently recognized species. It is possible, therefore, that overall species diversity in the group exceeds that based on the traditionally used characters of the wing (see Discussion). The genitalia of *H. hyppason* differ so drastically from other *anchisiades* Group members that we and Dr. Keith S. Brown (pers. comm.) have agreed that it should no longer be considered part of the Group. In addition, Hancock (1983) listed the taxon *dospassosi* Rütimeyer in the *anchisiades* Group. Known only from the holotype (AMNH), and not examined by Hancock, dissection of this specimen has shown it to represent the genus *Protesilaus* (Tribe Leptocircini *sensu* Hancock, 1983) (Johnson, Matusik and Rozycki, 1986). Omitting *hyppason* and *dospassosi,* clustering based on the characters of Table 1, along with consideration of female genitalia, suggests the following subgroups as most appropriate within the *anchisiades* Group: (1) *chiansiades, rhodostictus* complex; (2) *epenetus, pelaus, oxynius*; (3) *erostratinus, erostratus*; (4) *isidorus* complex, *maroni,* the new species *matusiki*; (5) *anchisiades* complex, *pharnaces, rogeri.*

Table 1 indicates that among the wing and genitalic characters diagnostic for species level taxa in the *anchisiades* Group, the Caripito specimen exhibits one wing and two genitalic characters unique to it. In addition, it shares one character with *H. isidorus* and *H. maroni,* one with *H. isidorus* and some taxa presently (perhaps incorrectly) placed as subspecies of *H. rhodostictus,* and one with eight other con-

Fig. 2. Geographic ranges of species and subspecies of the *Heraclides anchisiades* species Group (D'Abrera, 1981). Data from specimens in AMNH and collections of the junior author.

Table 1. Characters of *H. matusiki* ○; other *anchisiades* Group members ●; structure modified so as to make character distinction inapplicable ◑.

	CHIANSIADES	RHODOSTICTUS	EPENETUS	PELAUS	OXYNIUS	EROSTRATINUS	EROSTRATUS	ISIDORUS	MARONI	MATUSIKI	ANCHISIADES	PHARNACES	ROGERI
WING UPPER SURFACE													
Yellow Postmedian Bands, Both Wings; White Marginal Chevrons				●									
As Above, but Hindwing Only						●	●						
No Bands, Chevrons Only			●		●								
Red Postmedian Bands, Hindwing; Yellow Marginal Chevrons												●	
Large Red Elipses, Hindwing; Usually with White Postmedian Forewing Patch	●	●						●	●		●		●
Large, Cream-White Elipses, Hindwing; with Postmedian Forewing Patch										○			
MALE GENITALIA													
Valve, Terminal Tooth Centrad	●	●	◑	●	●	●	●	●	●		●	●	●
Valve, Terminal Tooth Ventrad			◑							○			
Valve, Terminal Serrations Dorsad Tooth Only					●	●	●	●	●	○			
Valve, Terminal Serrations, Dorsad and Ventrad Tooth											●	●	●
Valve, Terminal Serrations Lacking	●	●	●	●									
Aedeagus Very Curvate	●		●	●		●	●		●		●	●	●
Aedeagus Mildly Curvate		●			●			●					
Aedeagus Straight										○			
Socii Open								●	●		●		●
Socii Closed	●	●	●	●	●	●	●			○		●	

geners exclusive of *H. anchisiades, H. isidorus, H. maroni* and *H. rogeri.* Although the overall wing shape and pattern of the Caripito specimen is most suggestive of *H. anchisiades,* the former's unique wing character (large cream-white hindwing orbs) is approached only by specimens from a few populations of *H. isidorus* and *H. rhodostictus* in Columbia and Ecuador. Considering the above, and that the Caripito specimen comes from an area in which natural habitat may now be extirpated, we propose the following:

Heraclides matusiki, new species

Figs. 1A–B, 3H, 5A–D

Diagnosis. General maculation pattern like taxa of groups (1), (4) and (5) referenced above and in Figure 1; easily recognized by the two large cream-white orbs on the hindwing upper surface in vein interspaces distad vein M_3 (Fig. 1A, B), all other taxa in groups (1) and (5) having red to red-orange orbs (Fig. 1C, D, G, F), as do taxa of group (4) except for a few populations (Ecuador to Colombia) with white to yellow orbs about one-fourth the diameter of those on *matusiki* (Fig. 1E, H); hindwing under surface with a broken orange postdiscal arc of spots (obsolescent cephalad) and the spot of cell M_3 occurring distad in row with the large ellipses, other taxa with postdiscal spots red, with spot of cell M_3 located basad at the discal veins (*isidorus* complex and *rogeri*), or with all spots enlarged (*anchisiades* complex); antennae orange dorsad, not black as on all other taxa. In the male genitalia (1) *matusiki* (Figs. 3H, 5A) with terminal tooth of harpe nearly contiguous with harpe's ventral surface, (2) *matusiki, isidorus* (Fig. 3E, F), *maroni* (Fig. 4H), *erostratus* (Fig. 3B) and *oxynius* (Fig. 3A) with terminal serrations limited to dorsad of harpe's terminal tooth (other taxa as reviewed in Table 1, Figs. 3, 4 and 5B, C); (3) *matusiki* (Figs. 3H, 5D) with aedeagus straight, similar only to the mildly curvate aedeagii of some taxa of *isidorus* complex (Figs. 3E, F, 5E) and *rhodostictus* complex (Fig. 3J, K).

Description. MALE. Upper surface of the wings: forewing dark brownish black basad the postmedian area, noticeably lighter distad; powdered white ovate patch distad of postmedian area in cell CU_2. Hindwing uniformly as dark as basad area of forewing; two large postmedian cream-white ellipses in discal through postmedian area of cells CU_1 and CU_2 with adjacent areas of cells 2^A and M_3 having oblong parallel cream-white patches. Crennated margin without white chevrons except in cells RS and M_1. No taillike extension of vein terminus CU_1. Under surface of the wings: forewing as on upper surface but with powdered white ovate patches in both cells CU_2 and CU_1. Hindwing with large postmedian ellipses of cells CU_1 and CU_2 bright white, edged orange distad and with complementary smaller bright orange spots occurring as two in cell 2^A (postmedian and discal), one in cells CU_1 and CU_2 (postdiscal), and variously obsolescent cephalad to the costal margin (postmedian). An orange line is apparent in cell 2^A at the margin and on all vein termini thence to vein CU_1. Length of forewing: 53.0 mm (holotype). *Male Genitalia.* Figures 3H, 5D. Overall configuration as in other members of species group but differing markedly as follows: aedeagus straight, not curved; terminal tooth of valval harpe nearly contiguous with ventral surface of harpe; socii closed (see Diagnosis and Remarks).

FEMALE. Unknown.

Holotype. ♂ (Fig. 1A, B). Venezuela, Caripito, 7 January 1912, ex. collection New

York Zoological Society Tropical Research Department, William Beebe, Director; deposited AMNH.

Distribution. Known only from the type locality, adjacent to the isolated montane region characterizing the Sucre State in eastern Venezuela. The area of Caripito is vastly more populated today than in 1912. It is therefore possible that if the original distribution area of *H. matusiki* was highly insular, the species may be extinct.

Etymology. The species is named for David Matusik who first noticed it in AMNH holdings and in recognition for his discoveries of several new and unusual Papilionidae, including *Graphium meeki inexpectatum* L. & J. Miller, the type gender of *P. diaphora,* the species status of *Papilio huanucana* (de Luque) and the life history of *Papilio machaonides* Esper.

DISCUSSION

Taxonomic Characters of the anchisiades *Group*

Valvae. Hitherto, most students of Papilionidae (Munroe, 1960; Hancock, 1983; Beutelspacher and Howe, 1984) have utilized characters of the valval harpe in the diagnosis of species level taxa. In the *anchisiades* Group each of the species evidences a distinct caudal configuration of the harpe. There is a variously located terminal tooth, with or without serrations located dorsad and/or ventrad. As noted in Figures 3–5, there is apparent overlap in the species-distinctive configurations (summarized in Table 1) within and between several of the "subspecies" now associated with the *H. isidorus* and *H. rhodostictus* complexes. This suggests either misassociation of some of these trinomens or the possibility that several sympatric species occur in these complexes in Colombia and Ecuador. *Aedeagii*: Several species within the *anchisiades* Group possess distinct aedeagii, though the generalized configuration of the group is a mildly curvate structure. *H. matusiki* appears distinct in having a straight aedeagus (Figs. 3H, 5D), while *H. maroni* evidences a similarly unique radically curvate structure. Since both species appear to be highly insular, these characters strongly suggest specificity. *Socii:* Some consistent differences are notable among the various species clusters with the *anchisiades* Group. However, the taxonomic utility of these differences (Figs. 3–5, Table 1) is uncertain. Characters of the socii have not been widely used by papilionid workers. Notwithstanding, our study of the *scamander* Group of *Pterourus* (Tribe Papilionini *sensu* Hancock, 1983; Johnson, Matusik and Rozycki, 1985) showed significant socii differences among the species of this group. In the *anchisiades* Group socii have two overall configuration—(a) an apparent "open" lateral configuration [idealized by vertical hatching in Figs. 3–4] in which the outer lateral wall of the socii are variously transparent with sclerotized portions of the inner lateral wall showing markedly through and (b) an apparent "closed" lateral configuration in which the outer lateral wall is sclerotized thickly and obscures any view of the inner lateral wall.

Species Status of H. matusiki

We apply the species category to *matusiki* because of the variety of characters which distinguish its holotype from all presently known congeners (see Diagnosis and Table I). If the majority of characters in *H. matusiki* approximated those of a particular described taxon, we might have suggested *matusiki* as a subspecies thereof.

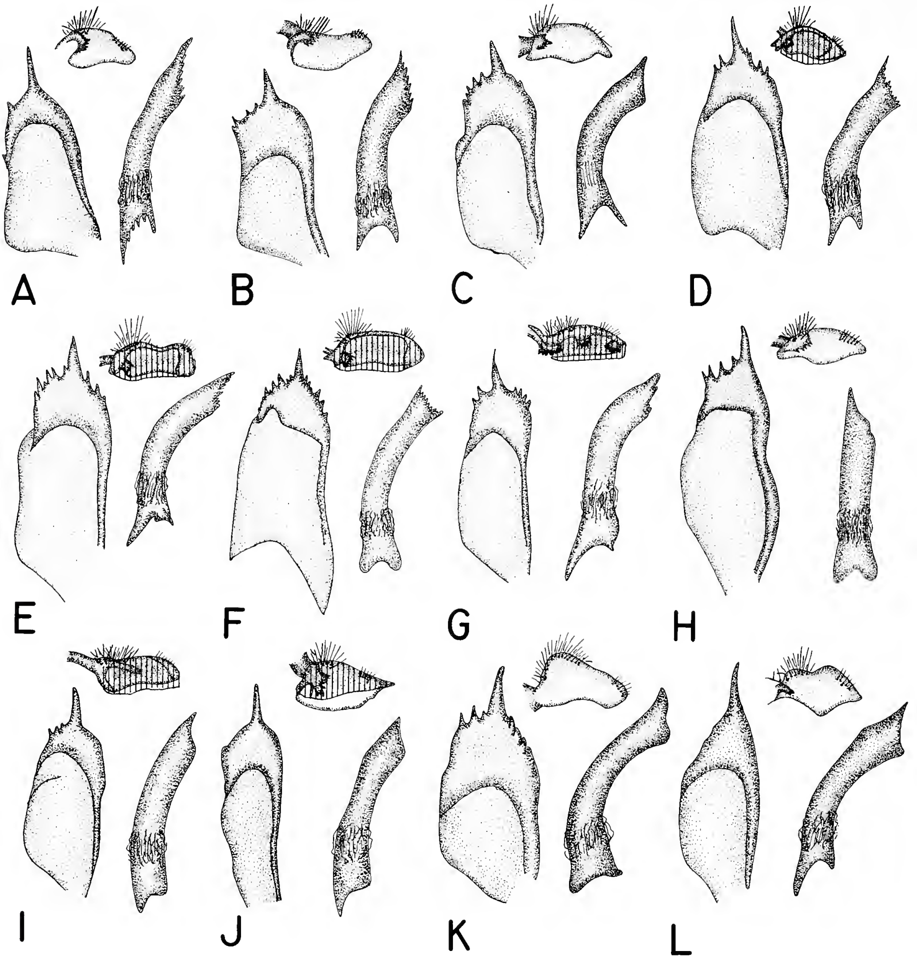

Fig. 3. Male genitalia of *Heraclides anchisiades* species Group. Format—above each letter, left, harpe of valve, inner lateral view; right, aedeagus, lateral view; center, above, socii, outer lateral view. Dissections all AMNH, locality of figured specimen listed first with number dissected in parentheses following, additional localities and number in brackets thereafter. A—*oxynius,* Cuba (3); B—*erostratus,* Guatemala (3) [Verapaz, Guatemala (1)]; C—*erostratinus,* Jalapa, Mexico (3) [Veracruz, Mexico (1)]; D—*anchisiades anchisiades,* Paramaribo, Surinam (3) [Port-of-Spain, Trinidad (1); Jantun-yacu, Ecuador (1); Bogotá, Colombia (1); Iquitos, Peru (1)]; E—*anchisiades idaeus* (Fabricius), Oaxaca, Mexico (3) [Guatemala (1); Honduras (1); Barro Colorado, Panama (1); San Jeronimo, Chiapas, Mexico (1)]; F—*anchisiades capys* (Hübner), Santa Catarina, Brazil (3) [Misiones, Argentina (1); Santisima-Trinidad, Paraguay (1); Bolivia (1); Caviuna, Brazil (1)]; G—*rogeri,* Pisté, Mexico (3); H—*matusiki,* Caripito, Venezuela (1); I—*isidorus isidorus,* Lima, Peru (3) [Rio Seco, Peru (1); Tingo Maria, Peru (1); Rio Huallaga, Peru (1)]; J—*isidorus brises* Colombia (3) [Cauca Valley, Colombia (1); Yellow-orbed *isidorus* (unnamed population), Colombia (2)]; K—*pharnaces,* Morelos, Mexico (3) [Chiapas, Mexico (1)]; L—*epenetus,* Balzapamba, Ecuador (3).

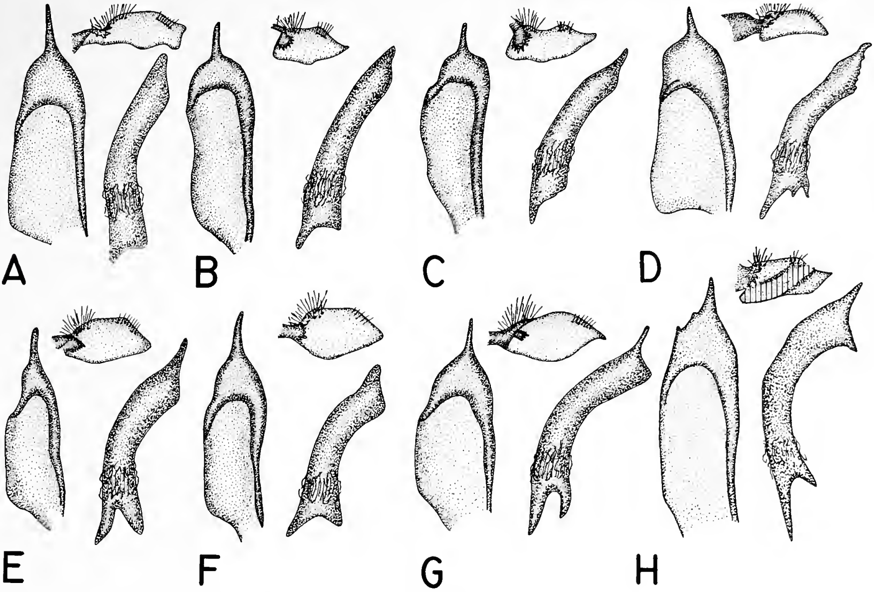

Fig. 4. Male genitalia of *Heraclides anchisiades* species Group (cont.). Format as in Fig. 3. A—*chiansiades,* Janjui, Peru (3) [Rio Ortequaza, Colombia (1); Jantun-yacu, Ecuador (1)]; B—"*rhodostictus*" *flavescens* (ssp. usually associated with *isidorus*) Huagra-yacu, Ecuador (3) [Abitagua, Ecuador (1); yellow-orbed *rhodostictus* (unnamed population), Ecuador (1)]; C—*rhodostictus pacificus,* Colombia (3) [Guamoco, Colombia (1)]; D—*rhodostictus rhodostictus,* Rio Grande, Honduras (3); E—*pelaus pelaus,* Jamaica (3); F—*pelaus imerius* (Godart), Adjuntas, Puerto Rico (3); G—*pelaus atkinsi* (Bates), Havana, Cuba (2); H—*maroni,* French Guiana (1) [AME].

To do this, however, when characters of *H. matusiki* are either unique or variously shared with several other species of the group, would imply that characters used to define species within the group (especially genitalic characters) have no utility. The latter is not the case according to the data reviewed herein.

The variety of specialists' opinions concerning status and affinities of *matusiki* results less from the uniqueness of the holotype than from methodological differences. How to apply the International Code of Zoological Nomenclature (ICZN) obligatory categories in neotropical taxa is currently a subject of debate in lepidopterology. Generally, South American lepidopterists construe any evidence of possible wild-caught hybrids as indicative of subspecies status in the inferred parent taxa (Keith S. Brown, Jr., pers. comm.). Further, the hypothesis of Pleistocene "refugia" is generally accepted as the major historical factor underlying contemporaneous taxonomic and distributional relations (see, for instance, Pranz et al., 1982). As a result South American lepidopterists generally choose to view poorly known or little studied populations (or specimens) as representing subspecies of the most geographically proximate congener. Such a method is in the best sense utilitarian, considering that most Neotropical butterfly groups have received little morphological study. Further, such studies do not always offer reliable taxonomic characters. Preparation of a

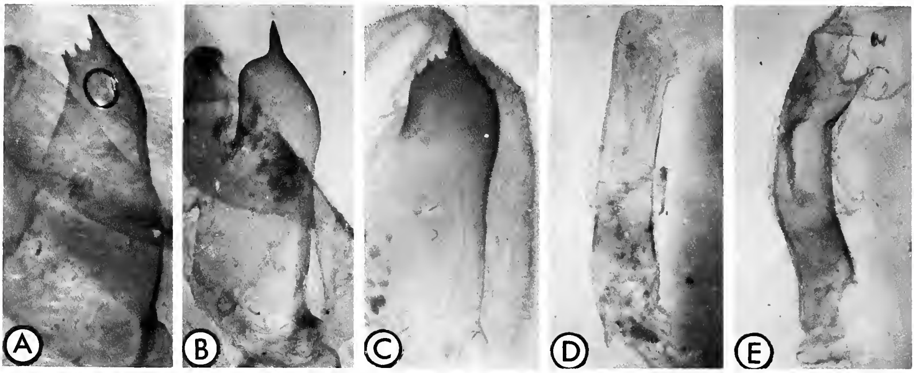

Fig. 5. *Heraclides anchisiades* species Group, particular features: A: valval harpe (with rest of valve folded back) *H. matusiki,* inner lateral view; B: same, *H. isidorus,* Ecuador, specimen with small white postmedian spots [see Fig. 1, E4 and H4, and Diagnosis] as with taxon *flavescens* perhaps best associated with *rhodostictus*; C: same, *H. anchisiades anchisiades,* Parimaribo, Surinam, regionally sympatric with *H. matusiki*; D: aedeagus, lateral view, *H. matusiki*; E: aedeagus, lateral view, *P. isidorus brises,* Colombia.

synonymic list of Neotropical Papilionidae by South American lepidopterists is currently in progress and will have involved a significant amount of morphological investigation (Keith S. Brown, Jr., pers. comm.). However, the view of apparent wild-caught hybrids and historical processes will affect the opinions on synonymy. Other methods (e.g., cladistics, or vicariance biogeography) would not construe possible wild-caught hybrids as indicative of subspecies categories. Further, with sufficient morphological evidence, this view might also reject lumping with the most geographically proximate congener and, instead, propose a species level taxon with an apparent vicariant sister taxon. Concerning *H. matusiki* and *H. maroni,* and data summarized in Table 1 and *Diagnosis,* it is reasonable to consider these two taxa as eastwardly distributed sister species of the *H. isidorus* complex. However, given current views from which most common taxonomic usages for Neotropical taxa are derived, we suspect that most South American lepidopterists will come to view both *H. matusiki* and *H. maroni* as subspecies of *H. anchisiades.*

ACKNOWLEDGMENTS

Numerous specialists and museum curators aided in discussing data, reviewing manuscripts of searching collections. Below, we list these persons, noting after each the collection surveyed: Dr. Keith S. Brown (Collection Universidade Estadual de Campinas, São Paulo, Brazil; Museu Nacional, Rio de Janeiro, Brazil; Collection Ernesto W. Schmidt-Mumm, Bogotá, Colombia; Collection Museo de Historia Natural "Javier Prado," Lima, Peru); Dr. Tommaso Racheli (Collection Instituto de Zoologia Argricola, Maracay, Venezuela; Collection Tommaso Racheli); Dr. Ernesto W. Schmidt-Mumm (Collection Ernesto W. Schmidt-Mumm); Dr. Olaf H. H. Mielke (Collection, Dep. de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil); Dr. Lee D. Miller (Allyn Museum of Entomology of the University of Florida, Sarasota, Florida, U.S.A.); Dr. H. T. Hannemann (Zoologisches Museum der Humbolt Universität, Berlin, Germany); Dr. Rienk de Jong (Rijkmuseum van Natuurlijke Historie, Leiden, Netherlands); Dr.

John H. Rawlins (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.), Dr. Robert K. Robbins (National Museum of Natural History, Washington, D.C., U.S.A.). Philip Ackery [British Museum (Natural History), London, United Kingdom] responded that the specimen seemed unfamiliar but staff lacked time to make a detailed search. In addition we used the collections of David Matusik (Skokie, Illinois), that of the junior author and one anonymous commercial dealer who retains significant holdings in unusual Papilionidae.

In regard to our treatment of the *anchisiades* Group, Dr. Keith Brown kindly reviewed drafts of the manuscript as well as suggested and/or contacted for us numerous of the above listed workers or collections. We are most grateful for his generous assistance in this regard and any apparent disagreements over the content of this paper are purely scientific. Dr. Lee D. Miller discussed this project with us on several occasions and Dr. Ernesto W. Schmidt-Mumm and Dr. Tommasso Racheli also kindly considered draft manuscripts or materials of this study. Two anonymous reviewers made very helpful comments concerning the paper and Dr. Randall T. Schuh (AMNH) made numerous helpful suggestions concerning methods and procedures. Dr. Frederick H. Rindge (AMNH) kindly has facilitated access to AMNH papilionid holdings for Mr. Matusik and the junior author.

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Received July 19, 1984; accepted December 23, 1985.

J. New York Entomol. Soc. 94(3):394–408, 1986

MIMICRY OF ANTS OF THE GENUS *ZACRYPTOCERUS* (HYMENOPTERA: FORMICIDAE)

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Abstract.—Within the myrmicine ant genus *Zacryptocerus* 13 of 21 species in Central America are hypothesized to be models for a Batesian mimicry complex that includes at least 40 species of arthropods. The ants are striking in appearance because they are strongly flattened and silvery in color, and use chemical defenses against potential predators, although they are eaten by ant specialists and as reproductives. The ants nest and forage arboreally and most of the identified mimics used dead branches in some way. The larger number of mimetic species than models appears possible because of the abundance of the ants and the relative rarity of the mimics; the rarity is further enhanced by the host specificity of most of the mimics, supporting a model proposed by Brower. Mimics appear to become absolutely and relatively more numerous toward the equator. The selective agents ("operators") are thought to be generalist insectivorous birds; ant specialists are argued not to affect evolution of the system.

Collection of beetles of the genus *Agrilus* (Buprestidae) in southern Central America and their subsequent study in museum collections (Hespenheide, 1974, 1979, and unpublished) has revealed a set of species from different species groups that possess a common pattern of color and pubescence. Members of other families of beetles, Hymenoptera, Heteroptera, and spiders with similar patterns were also discovered through field collections, museum study, and review of the literature. The beetles appear to be ant mimics with a specific type of model. Ants are involved in mimicry complexes with other insects and spiders in at least three different ways ecologically (Edmunds, 1974; Reiskind, 1977; Rettenmeyer, 1970): 1) as typical Batesian models for less well defended mimetic forms; 2) as models for insects which live as commensals with the ants (Wasmannian mimicry); or 3) as models for spider predators of ants (Peckhammian mimicry).

The rather large number of distinctively patterned species involved in this mimetic complex recommend the present study, which is also intended to raise some additional questions, both about ant mimicry and about mimicry in general. My collections and experience with both models and mimics have been restricted to Central America and most comments will concern species which occur there, although the system occurs and likely is as much or more complex in South America.

THE MODELS

The ant models were easily identified as belonging to the myrmicine genus *Zacryptocerus* (sensu lato, Kempf, 1973; includes species referred to in earlier literature as *Cryptocerus* and *Paracryptocerus*) of the tribe Cephalotini. The Cephalotini are known as models of mimetic spiders (Reiskind and Levi, 1967). Nevermann (1930) independently pointed out the resemblance of his *Ethelema costaricensis* (Colydiidae) to *Zacryptocerus multispinosus biguttatus* (Emery) (under the synonym "*Cryptocerus gibbosus* Fr. Smith"; Kempf, 1972), Vogt (1949) mentioned the resemblance of *Agrilus ornatulus* Horn to *Zacryptocerus texanus* (Santschi), and Ekis (1976) noted the similarity of his *Enoclerus canus* (Cleridae) to *Zacryptocerus cristatus* (Emery).

The tribe Cephalotini consists of four genera containing about 113 species of ants (Kempf, 1972), of which 3 genera and 30 species occur in Central America. This paper will consider only the genus *Zacryptocerus,* although the genera *Cephalotes* is (Reiskind, pers. comm.) and *Procryptocerus* may be involved in mimicry complexes of their own. *Zacryptocerus* includes 21 species and one additional subspecies in Central America, all of which belong to the group of species previously placed in *Paracryptocerus* (Kempf, 1972; Snelling, unpublished); three species reach the United States (Smith, 1947), and 49 additional species are known from South America.

Zacryptocerus species have worker, soldier and reproductive castes, of which only the workers are considered in detail in this paper. *Zacryptocerus* workers of a given species are relatively uniform in size and coloration. Species tend to fall into one of three or four groups based on visually distinct facies; of these, the one including the largest number of species serves as a model for the mimetic forms described here. Species of this group are characterized by a strongly flattened and broad body form and head, and by an integument that is predominantly black but that is more or less densely covered with white scales which give an overall silvery-grey appearance (Fig. 1). Among the 21 Central American species, three (the "*wheeleri* group," Snelling, 1968; Fig. 2) are narrower, lack the conspicuous scales, do not therefore look very conspicuously different from other black ants, and seem to lack mimics (see discussion below). A fourth species *Z. umbraculatus* (Fig. 3) is predominantly red in coloration and has a darker gaster distinctly marked with yellow; it may be involved in other mimicry complexes, but will not be considered further here. Of the 17 remaining species, three are poorly known (*Z. basalis, bimaculatus,* and *sobrius*) and one is often predominantly reddish (*Z. pallens*), so that the following discussion will focus on 13 species which likely serve as models: *Z. aztecus* (Forel), *christophersoni* (Forel), *cristatus, curvistriatus* (Forel), *foliaceus* (Emery), *maculatus* (Fr. Smith), *minutus* (F.), *multispinus* (Emery), *multispinosus* (Norton), *porrasi* (Wheeler), *scutulatus* (Fr. Smith), *setulifer* (Emery), and *texanus.*

WHY MIMIC *Zacryptocerus*?

Of the three types of ant mimicry, only Batesian mimicry is an option for *Agrilus* and most of the other mimics discussed here, in that the mimetic species usually feed on wood and not inquilines or predators on ants. The distinctive appearance of *Zacryptocerus* is not itself sufficient basis for the convergent (or advergent—see Brower and Brower, 1972) evolution of mimetic forms—i.e., as a model for a Batesian mimicry complex—there must also be some basis for avoidance of the ant model by a somewhat generalized insectivorous predator potentially common to both the ant and any would-be mimic. Edmunds (1974), Reiskind (1977), and Rettenmeyer (1970) have pointed out that ants are often models for Batesian mimicry complexes because of any or all of three characteristics dissuasive to predators: 1) poisonous stings; 2) biting mouthparts, in some cases accompanied by chemical irritants; and/or 3) distastefulness, sometimes associated with pheromone systems. The primary defense of

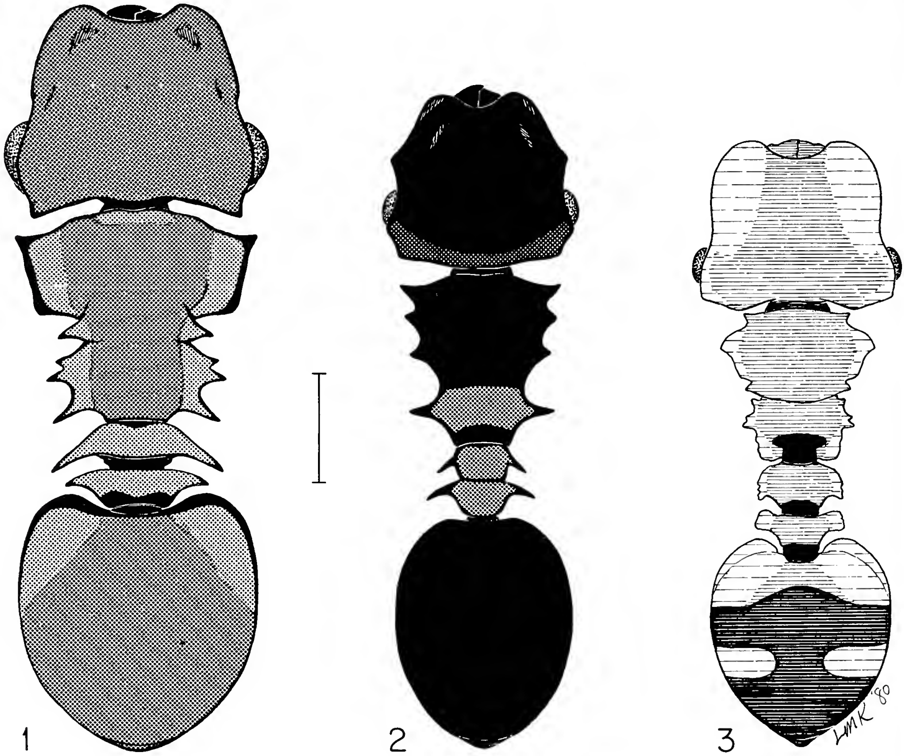


Fig. 1–3. Species of *Zacryptocerus*. 1. *Z. cristatus*. 2. *Z. rohweri*. 3. *Z. umbraculatus*— only *Z. cristatus* serves as a model for the mimicry complex described here. Scale indicates 1 mm.

Zacryptocerus seems to consist in distastefulness; they do not seem to have a sting of any consequence (unlike the predatory Ponerinae or the aggressive *Pseudomyrmex*; Janzen, 1966), and their mandibles are relatively small (Coyle, 1965). Coyle (1966) has studied the defensive behavior of three species of *Zacryptocerus* (*multispinosus biguttatus, multispinus,* and *umbraculatus*) in Costa Rica and found that, other than freezing or moving away, all three used chemicals released from the gaster or oral region as their primary defense. Workers picked up by me in the field for collection or examination typically have a very strong odor. In *Z. multispinus* an additional defensive maneuver consists of curling up into a ball so as to expose spines on the lateral margins of the thorax and petiolar segments. These defenses are not successful against all insectivorous birds: a specimen of the woodcreeper *Dendrocolaptes souleyetii* collected in Costa Rica by D. R. Paulson had consumed 9 *Zacryptocerus* workers and soldiers of two species (*multispinosus biguttatus* and *umbraculatus*) among 61 ants and 67 total prey (see discussion below). T. W. Sherry (1984) found small numbers of reproductive *Zacryptocerus* taken by several species of Tyrannidae in lowland Costa Rica, but this is not relevant to a mimicry system based on worker models.

ECOLOGY OF *Zacryptocerus*

Zacryptocerus is an arboreal ant that is characteristic of wet tropical forests, but also occurs into the subtropics as far north as the southwestern United States and extreme southern Florida (Smith, 1947). Members of the genus exhibit strongly dimorphic worker and soldier castes, and the latter are textbook examples (e.g., Wilson, 1971: 160f; also Creighton, 1963) of the highly specialized phragmotic defense of the nest. The biology of these ants has been studied in some detail for two species found in the United States, *Z. texanus* (Creighton and Gregg, 1954; Creighton, 1963) and *Z. rohweri* (Creighton and Nutting, 1965), and for several Costa Rican species (Coyle, 1965 and unpublished). Additionally, Wheeler (1942) lists a number of nest site records for members of the genus. Adults regularly forage on leaves or, more frequently, run on trunks and branches. In mature forests colonies are primarily in the canopy (Coyle, 1965), as evidenced by their being observed in numbers on recent tree falls or blowdowns. Colonies may be divided among a number of nests (Coyle, 1965; Creighton, 1963) and are commonly in dead branches. Creighton (1963) and Creighton and Nutting (1965) record nests of *Z. texanus* and *Z. rohweri* in the old larval burrows of smaller wood-boring beetles, including the Buprestidae, and the distinctive shape of the emergence hole figured (Creighton, 1963) for one nest suggests that it is a burrow of *Agrilus* (see below). Probably because of the defensive rather than aggressive nature of these ants, no species have been identified as obligate plant-ants (in the sense of Janzen, 1966), although Janzen (1974) records the genus as one of five using the swollen-thorn *Acacia ruddiae* Janzen, an atypical forest species which lacks a consistent association with *Pseudomyrmex,* and Wheeler (1942) reports nests in other ant-plants. As arboreal ants *Zacryptocerus* are peripheral participants in other ant-plant mutualistic systems: Wheeler (1910) reports Muller's observation of *Zacryptocerus* species visiting bead glands of *Bunchosia*; and *Zacryptocerus* spp. visit extrafloral nectaries of *Bixa orellana* L. (Bentley 1977), *Ipomea carnea* (Keeler 1978), and *Byttneria aculeata* (Hespenheide, 1985a). Jeanne (1979) reports *Z. multispinus* at baits of wasp brood in Costa Rica and an undetermined *Zacryptocerus* at similar baits in Pará, Brazil. Overall, the microhabitat of *Zacryptocerus* seems to be primarily that of dead branches (the most common nest sites), secondarily that of living branches (for nest sites or trails), and finally of leaf surfaces (for solitary workers foraging, especially for pollen, nectar, and/or honeydew—Creighton, 1963; Creighton and Nutting, 1965).

MIMETIC INSECTS AND SPIDERS

Agrilus (Buprestidae)

As noted above, Vogt (1949) first pointed out the resemblance of a species of *Agrilus* to one of *Zacryptocerus.* Collection and study of species of *Agrilus* occurring or likely to occur in the region from Mexico through Panama have revealed 22 species of *Agrilus* that are marked in such a way that they resemble *Zacryptocerus* species. A number of other *Agrilus* are patterned in ways that resemble ants other than *Zacryptocerus.* The dorsal aspect of model species of *Zacryptocerus* (Fig. 1) is visually dominated by the broad head and gaster, both silvery-grey in overall appearance. Putative mimetic *Agrilus* (Fig. 4) typically combine the following characteristics: (1)

the head and pronotum shining black and more or less densely invested with white pubescence which yields an overall silvery appearance; (b) the anterior halves of the elytra deep matte black with a more or less complicated pubescent design of two or three transverse, oblique, and/or longitudinal bars; and (c) the posterior halves of the elytra again abruptly and densely pubescent, in some species then becoming sparser toward the apex. The overall effect is then a tripartite silvery/variegated/silvery, which corresponds to head/pronotum-and-petiole/gaster of the ants. Although a complete systematic study of the more than 600 species of Central American *Agrilus* remains to be made, it is clear that the mimetic forms belong to a number of different species groups within the genus and have therefore evolved independently. Table 1 lists the names of the described species considered to be mimetic, as well as the names of other insects and spiders in the complex. In addition to the Central American species, at least 7 South American *Agrilus* appear to mimic *Zacryptocerus,* including *A. dolatus* Kerremans and *A. esculentis* Fisher.

Only *Agrilus* among the Buprestidae has been identified with *Zacryptocerus*-like patterns, despite the similarity of ecology among most genera in the family (other than the leaf-mining forms). Absence of mimicry in other genera is likely due to their being either proportionately broader or larger overall than these rather small ants. Even among *Agrilus,* those 22 species which are mimetic of *Zacryptocerus* average significantly smaller in size than all 607 species recognized in the fauna (4.90 mm vs. 6.45 mm; $P_t < 0.001$).

Most *Agrilus* species are narrowly host-specific cambium miners in recently dead or dying wood (Fisher, 1928). Host range is typically a single plant species or several species within the same genus, rarely more than one genus (fewer than 10% of the species). Adults are found on branches of the host, especially those favorable as oviposition sites, or feeding on the leaves of the host, or, more rarely, on leaves or branches of plants near hosts. The size of adult *Agrilus* is related to the size of the branches mined by the larvae; i.e., smaller *Agrilus* bore smaller branches (Hespenheide, 1976).

Other Mimics

Field collections and study of the Biologia Centrali-Americana collection in the British Museum of Natural History has shown that a number of other groups of insects share the silvery/variegated/silvery pattern of *Agrilus* (Table 1, Fig. 5–9). Additional species in these and other families (e.g., Melasidae and Mordellidae) were not included in this discussion because they lack the precision of the pattern of those included—most frequently the middle region is alternatively simply black rather than variegated—although it seems likely that in some cases the resemblance would be effectively mimetic. The ecology of these other mimics is discussed briefly as follows:

Coleoptera. Anthribidae: This family as a group is commonly collected at tree falls where the larvae are presumably involved in feeding on fungi.

Bruchidae: Members of this family are seed predators (Janzen, 1969).

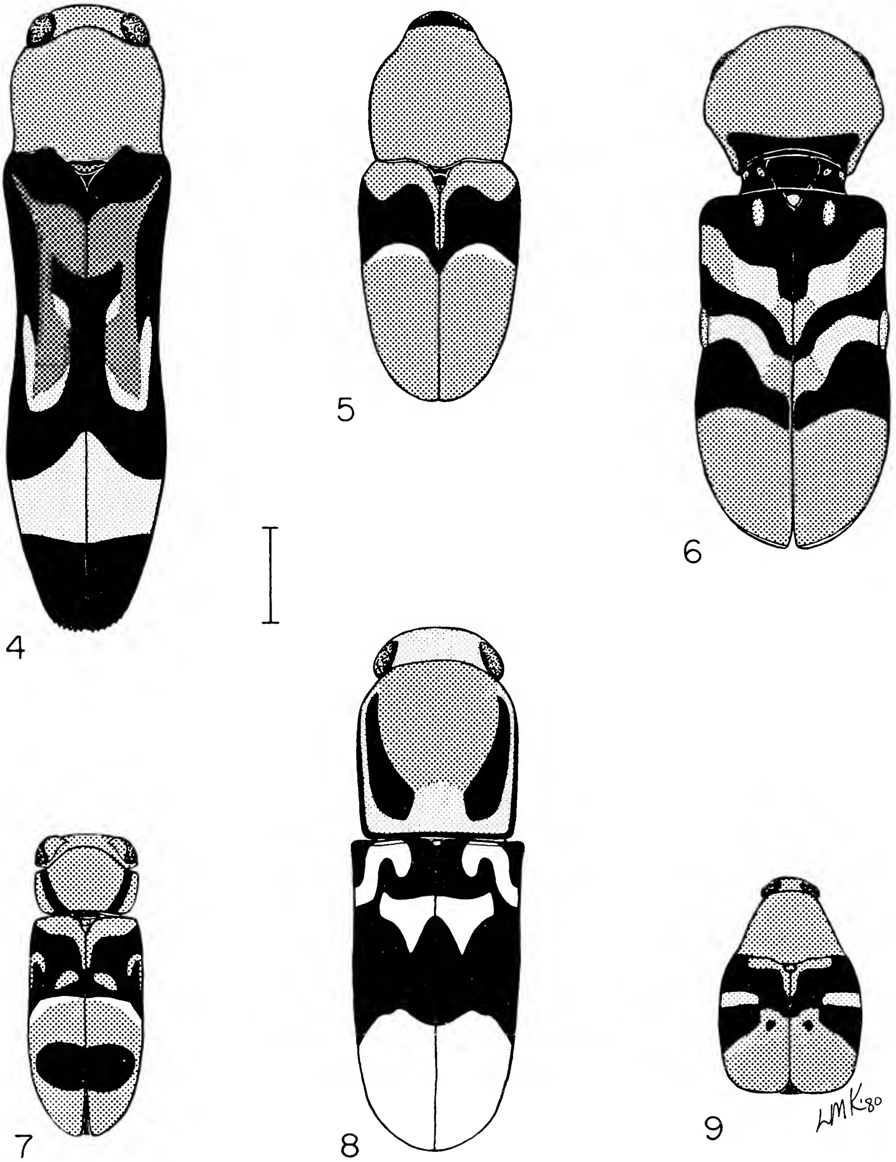
Cerambycidae: This family is infrequently involved in this complex probably for the same reason as are larger Buprestidae as well as because of their nocturnal activity periods. Chemsak and Linsley (1978) guessed that *Pseudotapnia* was an ant mimic from its unusual morphology. South American Cerambycidae in the British Museum

Table 1. Arthropods mimetic of *Zacryptocerus* ants in Central America.

Taxon	# spp.	Names of described species
Coleoptera		
Anthribidae		
Eugonops	1	*championi* Jordan
Eugonus	1	*decorus* Jordan
Bruchidae		
Acanthoscelides	1	*suaveolus* Sharp
Buprestidae		
Agrilus	22	*blandulus* Guerin, *buscki* Fisher, *lautuellus* Fisher, *ornatulus* Horn, *signatus* Waterhouse, *tezcatlipocai* Fisher, *titlaceabanae* Fisher
Cerambycidae		
Pseudotapnia	1	*curticornis* Chemsak & Linsley
Cleridae		
Enoclerus	2	*canus* Ekis, *cinereus* Gorham
Phyllobaenus	3	
Colydiidae		
Ethelema	2	*decorata* Sharp, *costaricensis* Nevermann
Curculionidae–Baridinae		
Coelonertus	1	*nigrirostris* Solari
Curculionidae–Zygopinae		
Eulechriops	1	*cylindricollis* Champion
Helleriella	1	*ruddiae* Hesphenheide
Cylindrocopturinus	1	*hainesi* Hespenheide
Hymenoptera		
Orussidae		
Ophrella	1	*lingulata* Middlekauff
Heteroptera		
Lygaeidae		
Neocattarus	1	
Araneae		
Salticidae		
Undet.	1	

that seem to be part of this complex include species under the following names there: *Aemylos triangulifer* Auriv., *Argyronides pulchella* Bates, *Epropetes cleroides* White, *Parazodes erythrocephalus.*

Cleridae: Clerids as larvae are predaceous on wood-boring beetles and are often found running on fallen trees. Interestingly, the genus *Epiphloeus* has not been found by me with a *Zacryptocerus* pattern, although it is an appropriate size, has rather complicated pubescent patterns, and is involved in other mimicry complexes (Hespenheide, 1973). Adult behavior differs significantly from *Enoclerus* and *Phyllobaenus,* however, in that adults are usually found sitting motionless on the vertical sides or undersides of branches, rather than running actively.



Figs. 4–9. Mimetic species of beetles. 4. *Agrilus ornatulus* (Buprestidae). 5. *Coelonertus nigrirostris* (Curculionidae, subf. Baridinae). 6. *Enoclerus cinereus* (Cleridae). 7. *Ethelema decorata* (Colydiidae); 8. *Eugonus decorus* (Anthribidae). 9. *Acanthoscelides sauveolus* (Bruchidae). Scale indicates 1 mm.

Colydiidae: As noted above, Nevermann (1930) noted the resemblance of his species *Ethelema costaricensis* to *Zacryptocerus.* He mentions collecting both insects on fallen trees and considers the possibility *Ethelema* is an inquiline of *Zacryptocerus* and thereby a Wassmannian mimic, but he concedes he has never seen a beetle associated with a nest of the ants and discusses the difficulty of finding such an association. Nevermann also mentions, however, that *Ethelema* was collected on logs already attacked by (a) species of Scolytidae. I have also collected colydiids in association with scolytids and/or platypodids, and it seems more likely to me the beetles are predators of these other wood-boring beetles.

Curculionidae: Most weevils of the subfamily Zygopinae are wood-borers, and I would guess that to be true of *Eulechriops cylindricollis* Champion and *Cylindrocopturinus,* although less certainly for the latter because its morphology is unusual in other details than overall appearance (Hespenheide, 1985b). On the other hand, *Helleriella ruddiae* is especially interesting because of its ecological association with *Acacia ruddiae* (Hespenheide, 1980; Janzen, 1974, see above) and, thereby, with *Zacryptocerus.* Specimens of *Helleriella ruddiae* were reared by Janzen from swollen thorns of the *Acacia* unoccupied by ants, as are other *Helleriella.* Other swollen-thorn *Helleriella* are somewhat ant-like in appearance, typically with reddish or blackish areas set off by narrow bands of white scales. It is especially interesting that in a species of *Acacia* that lacks *Pseudomyrmex,* the associated *Helleriella* has evolved a color pattern that is similar to that of one of the other ants that replaces *Pseudomyrmex,* albeit on a less regular basis. Other Zygopinae from Central America (*Lechriops albovariegata* and *canescens* Champion) and South America (*Mnemyne viduata* Pascoe, *Copturus mimetica* Hespenheide) suggest *Zacryptocerus* but differ in small details from the pattern narrowly-defined above.

Hymenoptera. Orussidae: Members of this family are typically parasitoids of wood-boring beetles, especially the Buprestidae.

Hemiptera-Heteroptera. Lygaeidae: Specimens of one species of *Neocattarus* were collected on leaves of bushes under a fruiting fig (*Ficus* sp.) where these bugs were feeding on fallen seeds (Slater, 1972). I have seen *Ficus* both at the Smithsonian Tropical Research Institute's Ancon headquarters and Barro Colorado Island station with colonies of several species of *Zacryptocerus.* Although I know of no reason for a consistent association of *Zacryptocerus* with *Ficus,* it appears to have been frequent enough for evolution of resemblance by the bug to the ant to have been to the advantage of the former. Although many of the *Neocattarus* were collected on the ground where most of the fruits were fallen, numbers of adults were also searching the leaves of bushes, presumably for seeds defecated by feeding birds. *Zacryptocerus* seems never to forage on the ground (Creighton, 1963), so that the advantage of the mimicry may accrue only to the smaller part of the population on aboveground vegetation, since the putative predators (see below) also forage off the ground.

QUESTIONS RAISED BY THE MIMICRY OF *Zacryptocerus*

Community Ecology of *Zacryptocerus* Mimics

The ecological unity of this complex centers on the use of dead branches. The model *Zacryptocerus* spp. nest in such branches. Of the 40 mimetic species listed in Table 1 and discussed above, 26 are wood-borers (including the ant-*Acacia* inhabitant

Helleriella), 8 are predators or parasitoids of wood-borers, 2 feed on fungi of dead wood, the spider is a solitary predator collected on a tree trunk, and 3 are seed predators or of unknown ecology. Of the 11 South American species known to me, all are wood-borers.

In the absence of evidence that any of the 40 species of mimics are themselves distasteful, they are all assumed to be Batesian mimics of the 13 widespread model species of *Zacryptocerus.* This imbalance in overall numbers of models and mimics raises the question of a differential in the relative population sizes of these groups as required of a Batesian mimicry relationship. Jackson and Drummond (1974) report four arthropod Batesian mimics of the arboreal ant *Camponotus planatus* in Belize, but found that the ant models comprised about 30% of individual arthropods collected from vegetation, whereas the four mimics comprised only 2% of the same samples. They also note that four species is the largest number of mimics reported for a single ant model. No attempt has been made here to associate particular mimic species with particular species of *Zacryptocerus*—although it might be partially possible on the basis of relative sizes—but the overall complex is certainly much larger than that for the *Camponotus.*

Although the number of mimetic species is greater than the number of model species, the abundance of *Zacryptocerus* worker individuals is certainly much higher than the cumulative abundance of their mimics in all habitats. Published colony sizes for *Zacryptocerus* range from as few as 27 (for *Z. texanus*; Creighton and Gregg, 1954) to as high as 752 (polydomus colony of *Z. multispinus*; Coyle, 1965), with as many as 694 for a single nest (Coyle, 1965). The related *Cephalotes atratus* occurs in colonies of more than 10,000 (Weber, 1957). Few of the mimetic species, on the other hand, are known from more than a half-dozen specimens from all museums combined, although under very favorable conditions they may be relatively numerous locally on a host plant (G. H. Nelson has collected a few dozen *Agrilus ornatulus* on its host *Sapindus,* and the *Neocattarus* were relatively abundant under the single *Ficus* tree during the brief fruiting period characteristic of species of the genus).

Zacryptocerus species are, of course, not specific to particular plant species, although they may favor certain species or genera; Creighton and Gregg (1954) report most *Z. texanus* nests from the live oaks *Quercus virginiana* and *Q. fusiformis,* and neotropical *Zacryptocerus* may favor *Ficus* (see above; also *Acacia ruddiae*) without being restricted to them.

The general ecological-demographic pattern of this mimicry complex therefore seems to be the following: A small number of model species range widely over the many plant species in the community and are locally numerous at nests of a few 10's or 100's of individuals. The mimics are primarily host-specific wood-boring or fungus-feeding beetles which are low in numbers, usually solitary, and restricted to the vicinity of their particular plant hosts. A smaller number of less numerous parasitoids and predators may range more widely. The larger number of mimetic species does not endanger the model-mimic ratio required of Batesian systems because of their regular dispersion over the community as a consequence of their host specific plant preferences. Interestingly, this pattern of distribution of mimics was predicted by Brower (1958) as a consequence of the ability of visually-hunting predators to form search images. Brower proposed his model in terms of closely-related and therefore

Fig. 10. Zones in Central America for biogeographical analysis (Table 2). Lines follow national or state (Mexico) boundaries. Zone 2 includes only states bordering on Mexico.

morphologically similar procryptic insects, which is analogous to convergently-similar Batesian mimics, and both share the primary requirement of narrow host plant specificity. Much of the theory and most examples of mimicry derive from free-flying and therefore relatively widely-ranging Lepidoptera. In the system described here, and in many other systems encountered in my study of *Agrilus* and ecologically related organisms, the more restricted mobility of the participating species (in this case especially of the models) allows a "structure" that almost certainly permits greater complexity to the system.

Biogeography of the Mimicry Complex

A variety of studies of marine (Bakus and Green, 1974; Palmer, 1979; Vermeij, 1978) and terrestrial organisms (Connell, 1970; Janzen, 1970; Elton, 1973), has produced evidence that suggests the intensity of predation increases toward the trop-

Table 2. Geographic distribution of *Zacryptocerus* models and *Agrilus* (Buprestidae) and other insect mimics.

			Mimics		
Zone[1]	Ants	Total spp.	*Agrilus* mimics (% fauna)	Others	Total
2	1	109	2 (0.8)	0	2
3	2	74	1 (1.4)	0	1
4	4	146	0	0	0
5	5	171	2 (1.2)	0	2
6	5	205	9 (4.4)	2	11
7	8	90	2 (2.2)	3	5
8	8	44	1 (2.3)	4	5
9	10	38	1 (2.6)	4	5
10	9	64	3 (4.6)	8	11
11	9	70	8 (11.4)	9	17
Total	17	607	22 (3.6)	15	37

[1] See Figure 10 for delimitation of geographic zones.

ics. One may divide Central America and the immediately adjacent portion of the United States into 11 geopolitical zones that are roughly cross sections of the Central American isthmus (Fig. 10). One may then compare the distributions of the 13 more common putative model species of *Zacryptocerus* (Kempf, 1972; Snelling, unpublished) with those of the mimetic species (various taxonomic studies, Hespenheide, unpubl.). The results of this comparison are presented in Table 2. The number of ants increase toward South America and so, in general, do the numbers of mimetic species.

The genus *Agrilus* accounts for the largest number of mimetic species but does not as a genus overall increase regularly in numbers of species toward the equator but, rather, peaks in Mexico and then declines. However, if one divides the number of mimetic *Agrilus* in each zone by the total number of *Agrilus* species in that zone (Table 2), the proportion of mimetic forms does increase more regularly. This might be taken as evidence of higher predation intensity as one moves toward the tropics, except that the increase in the proportion of species mimetic of *Zacryptocerus* is accompanied by both increases and decreases in the proportions of mimetic species involved in complexes with other models (e.g., Hespenheide, 1973, 1975a). The overall pattern is complex, but the highest proportions of mimetic species of all types are highest at the southeastern end of the geographical gradient and therefore consistent with the observations that marine invertebrates are more heavily defended in more tropical areas (Palmer, 1979; Vermeij, 1978).

There is a definite collection bias among non-*Agrilus* mimics to those areas I have collected (Costa Rica, Panama), so that the larger absolute numbers of mimics there cannot be taken as evidence for higher predation rates selecting for more sophisticated antipredator adaptations. The proportions of mimetic *Agrilus* are free of such a bias, in that non-mimetic species are collected as vigorously as mimics.

One interesting result of the biogeographic analysis is the difference in the presence of mimetic *Agrilus* up the eastern and western coasts of Mexico. On the east coast, *Z. texanus* has two *Agrilus* mimics (*lautuellus, ornatulus*) as far north as Texas. On the west coast, only the "*wheeleri*" group of *Zacryptocerus* is found north of Nayarit, and no mimetic *Agrilus* has been found to date north or west of the Federal District. This observation bears out the exclusion of that section of the genus from the complex and from the present discussion (see above) on the basis of its less distinctive morphology.

Relative Importance of Specialized vs. Generalized Insectivores

Turner's (1977) succinct question—"Who are the dupes?" (the "operator" in Vane-Wright's, 1976, classification of mimetic relationships)—is appropriate in view of the observations above that *Zacryptocerus* are fed on by some birds. Sherry (1984) found that flycatchers in lowland Costa Rica fed on reproductives, but reproductive ants in mating flights are widely eaten by birds (Thiollay, 1970) and are essentially unprotected compared to workers. The evidence from the single *Lepidocolaptes* stomach mentioned above suggests that species is a specialist on non-reproductive ants, and the presence of a soldier caste member suggests the bird fed on a nest rather than on solitary workers. As a forest-based, arboreal forager, *Lepidocolaptes* should take *Zacryptocerus* regularly. Woodpeckers other than *Colaptes* (see above, also Hespenheide, 1975b; Kilham, 1979), anteaters (Lubin et al., 1977), and lizards (Schoener, 1966) are also arboreally foraging specialists on ants, but also certainly constitute a minority among insectivorous organisms.

That some insectivores specialize on ants does not invalidate ant mimicry and would actually have little effect on the evolution of mimicry, apart from selecting for greater defenses by the ant models, since the mimicry would only be effective on generalist insectivores that would avoid distasteful (to them) ants in favor of other taxa. Looking like an ant might increase the risk of a mimic to an ant-eating specialist such as *Lepidocolaptes,* except that such specialists usually search out nests and colonies rather than solitary workers (Kilham, 1979). The relative importance of generalist insectivores *contra* specialists in the evolution of mimicry is thus analogous to the responses of herbivores to the evolution of plant chemical defenses: generalists are deterred whereas specialists are not (Rhoades and Cates, 1976).

Generalist insectivores which have the potential for encountering the greatest numbers of models and mimics in the habitat of both (see above) would be those foraging on branches and twigs. In Central America these would include primarily woodpeckers (Picidae), woodcreepers (Dendrocolaptidae), certain overbirds (Furnariidae, such as *Xenops, Premnoplex, Margarornis*), and the migrant black-and-white warbler (*Mniotilta*) among birds; *Anolis* and geckos among lizards; and certain tree-running mantids and reduviid bugs. The importance of vision likely restricts the important predators to the birds and lizards, and the readiness of at least some *Anolis* to eat ants (Schoener, 1966) may limit the number of appropriate lizards. Both the woodpeckers and wood-creepers include generalist as well as ant-specialist species (Cruz and Johnson, 1979; Hespenheide, 1975b, and unpublished) and, in terms of both numbers of species and relative abundance are probably the most important selective agents in the evolution of this mimicry complex, with the role of lizards being uncertain.

ACKNOWLEDGMENTS

Because these observations have accumulated over several years in conjunction with several other studies, many individuals and agencies have contributed to this summary. Among those with whom discussion of ideas was important was the late Robert Silberglied, himself interested in the mimicry of ants by beetles (Silberglied and Aiello, 1976) and in whose honor this paper is dedicated. Roy R. Snelling determined and shared insights on the ants and commented on the manuscript. Thomas W. Sherry shared unpublished data and made several helpful suggestions on the manuscript. Those who made or verified determinations include W. F. Barr, John Kingsolver, J. A. Slater, and B. D. Valentine. Howard Evans, then of the Museum of Comparative Zoology, Cambridge, and Richard T. Thompson of the British Museum (Natural History) were especially helpful during visits there. Margaret Kowalczyk prepared the figures. Financial aid and logistical support have been provided by the Organization for Tropical Studies, Smithsonian Tropical Research Institute, University of Connecticut Research Foundation, University of California Academic Senate, and the National Science Foundation (DEB 76-10109).

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Received January 29, 1985; accepted November 27, 1985.

J. New York Entomol. Soc. 94(3):409–415, 1986

THE FIRST OCCURRENCE OF THE SUBFAMILY ARTHENEINAE IN THE WESTERN HEMISPHERE WITH THE DESCRIPTION OF A NEW TRIBE (HEMIPTERA: LYGAEIDAE)

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Abstract.—The genus *Polychisme* Kirkaldy is reviewed. The type species *Imbrius ferruginosus* Stål is redescribed and recorded from Colombia and Venezuela. It is shown to be not congeneric with the only other species, *Pachymerus poecilus* Spinola, and is removed from the Ischnorhynchinae and placed in the Artheneinae as a new tribe, the Polychismini. *Polychisme poecilus* is placed in the genus *Syzygitis* Bergroth, accompanied by a discussion of its correct specific name. Illustrations of *Polychisme ferruginosus* include a dorsal view, details of the abdomen, genital capsule, and spermatheca.

Recently we have investigated the relationships of a number of taxa that had been placed in the Ischnorhynchinae. Among these was the Neotropical genus *Polychisme.* This genus, before our study, contained two nominal species, *Imbrius ferruginosus* Stål, originally described from Colombia, and *Pachymerus poecilus* Spinola, originally described from Chile and placed in *Polychisme* by Scudder (1962). *Polychisme* was a replacement name by Kirkaldy (1904) for *Imbrius* Stål (1874) which was preoccupied. The type species of *Imbrius* Stål was *Imbrius ferruginosus* Stål by monotypy, therefore, *ferruginosus* becomes the type species of *Polychisme.*

To our surprise, we discovered that not only are *ferruginosus* and *poecilus* not congeneric but, in fact, do not belong in the same subfamily.

One of the important characteristics of the subfamily Ischnorhynchinae is the dorsally placed spiracles. In *P. poecilus* the spiracles are located dorsally on the conjunctiva of all abdominal segments, as in other genera of Ischnorhynchinae (in another paper we will discuss the systematic position of various taxa of "Ischnorhynchinae" with dorsally placed spiracles). However, *P. ferruginosus* does not have dorsally placed spiracles on abdominal segments three through seven (Figs. 4, 5). The spiracles, to the contrary, are placed on the "sternal shelf," which is an integral part of the abdominal sternum. The spiracles are, thus, definitely ventral. Sweet (1981) indicated that for the Lygaeidae the plesiomorphic spiracle position is dorsal. If this is true, it excludes *ferruginosus* as a member of the Ischnorhynchinae because the position of the spiracles on the sternal shelf is apomorphic.

The question then is, to what subfamily does *ferruginosus* have its closest phylogenetic relationship? Before giving our interpretation, it should be explained that spiracle 2 is actually placed dorsally (or laterally) on the membrane between the tergum and sternum.

P. ferruginosus is not a member of the Rhyparochrominae because the suture between sterna 4 and 5 is not fused and it has a conjunctival membrane. Fusion of these sternites is the most important synapomorphy uniting the various taxa of Rhyparochrominae. *P. ferruginosus* also lacks head trichobothria, a feature found in most rhyparochromines (although probably a plesiomorphy).

There are only two lygaeid subfamilies with a spiracular arrangement similar to that found in *ferruginosus,* the Artheneinae and the Oxycareninae. To which, if either, of these does *ferruginosus* belong?

We believe the closest phylogenetic relationships are with the Artheneinae. The presumed synapomorphies are not compelling but are perhaps more parsimonius than the alternative (closest relationship to the Oxycareninae). *P. ferruginosus* lacks inner laterotergites and does not have a reduced trichobothrial pattern on sterna 5, 6, and 7. The first of these can be considered a synapomorphy (although a weak one because it is based on the loss of a character), and the second is a plesiomorphy relative to the condition in the Oxycareninae.

Additional features in which *P. ferruginosus* agrees with the Artheneinae and differs from the Oxycareninae is the presence in *ferruginosus* of a hamus in the hind wing and the explanate lateral border of the pronotum. None of these relationships are compelling, but we consider it preferable to place *P. ferruginosus* in the Artheneinae for the present rather than to erect an additional subfamily.

Slater, Woodward and Sweet (1962) recognized three tribes in the Artheneinae: the Artheneini Stål (Palearctic); Dilompini (Australian); and Nothochromini (New Zealand). (In the same paper these authors actually treat Nothochrominae also as a distinct subfamily). Malipatil (1977), after examining and describing the nymphs, supported the placement of *Nothochromus* at a tribal level within the Artheneinae.

The occurrence of this artheneine in the Neotropics means that the subfamily now is known from all major faunal regions (except Nearctic), and suggests that the Artheneinae have a Gondwanaland origin.

We feel, however, that *ferruginosus* cannot be assigned to any of the above tribes and erect for it a new tribe.

Polychismini, new tribe

Diagnosis.

1. Spiracles on sternal shelf rather than on sternum below shelf (Figs. 4, 5).
2. Elongate, slender coiled spermatheca without terminal bulb and attendant flanges (Fig. 3).
3. Antenniferous tubercles visible from above.
4. Very short bucculae.
5. Dorsal surface strongly and coarsely punctate.
6. Metathoracic scent gland auricle curving posteriorly.
7. Juga short and remote from apex of tylus.
8. Scutellum lacking paired carinae.

Because *P. ferruginosus* and *P. poecilus* are not congeneric and *ferruginosus* is the type species of *Polychisme, poecilus* must be treated under another generic name.

Bergroth (1921) described *Syzygitis reflexa* from Chile as a new genus and species. Slater (1967) synonymized this species with *Polychisme poecilus.* The generic name

Syzygitis, thus, is available and becomes the correct generic name to be used with *Pachymerus poecilus* Spinola. For the present we retain this genus in the Ischnorhynchinae.

It should be noted that Spinola (1852) described *Pachymerus hyalinatus* and *Pachymerus poecilus* in the same paper, the former on pages 148–149, the latter on page 149. *P. hyalinatus,* thus, has page priority. Signoret (1863) suggested that *poecilus* might be only a color variety of *hyalinatus,* but in 1885 he listed *hyalinatus* as a synonym of *poecilus.* Berg (1896) listed *poecilus* as a synonym of *hyalinatus.* Reed (1900) did the reverse, listing *hyalinatus* as a synonym of *poecilus.* Scudder (1962) also used the name *poecilus,* and synonymized *Imbrius chilensis* Haglund with it, without mentioning *hyalinatus.*

We consider this a good example of the ambiguity raised by using the rule of first revisor, versus the objectivity of using page and line priority. Did Signoret (1863) place *poecilus* as a junior synonym of *hyalinatus* by suggesting that it was a possible color variety, or did Signoret (1885) make *hyalinatus* a junior synonym by listing it as a synonym of *poecilus*? Berg and the other South American authors apparently thought the former; Scudder (1962) believed the latter. Given the ambiguity of the 1863 Signoret reference and the unambiguous nature of his 1885 treatment, we are inclined to believe that, acting as first revisor, Signoret (1885) established *poecilus* as the proper nomen for the taxon. *Syzygitis poecilus* Spinola, thus, is a new combination.

All measurements are in millimeters.

Polychisme ferruginosus (Stål)

Figs. 1–5

Description. General coloration dull yellowish (griseus) marked with dark red as follows: greater portion of head; anterior pronotal lobe (except for explanate lateral margins and collar), a conspicuous median macula and a pair of obscure streaks midway between meson and lateral margins on anterior one-half of posterior pronotal lobe; basal and lateral portions of scutellum; a conspicuous spot in middle of clavus at level of distal end of scutellum; a series of four small irregular maculae on corium placed obliquely from lateral corial margin at level of distal end of clavus, mesoanteriorly, with inner macula lying just within medius at level of middle of claval commissure; and a macula midway along apical corial margin and a larger one encompassing apex of corium. Membrane hyaline, with a series of dark brown spots. Venter of head and anterior lobe of propleuron and mesopleuron chiefly black (but shading to reddish yellow dorsally and strongly pruinose giving a gray appearance interspersed with coarse, shining, black punctures), strongly contrasting with bright-yellow acetabula, metathoracic scent gland auricle, and posterior lobe of metapleuron. Abdominal sternum dark red brown with strongly contrasting rectangular pruinose "blocks" on sterna 2–6 and pruinose spots surrounding lateral trichobothria. Legs yellow, with brown on all femora except proximal and distal ends, and suffused areas on tibiae and third tarsal segments. Antennal segments one and two dull reddish, strongly contrasting with dark chocolate brown to almost black coloration of segments three and four. Body coarsely punctate above, on head, and pronotum below. Mesosternum smooth, black, and polished.

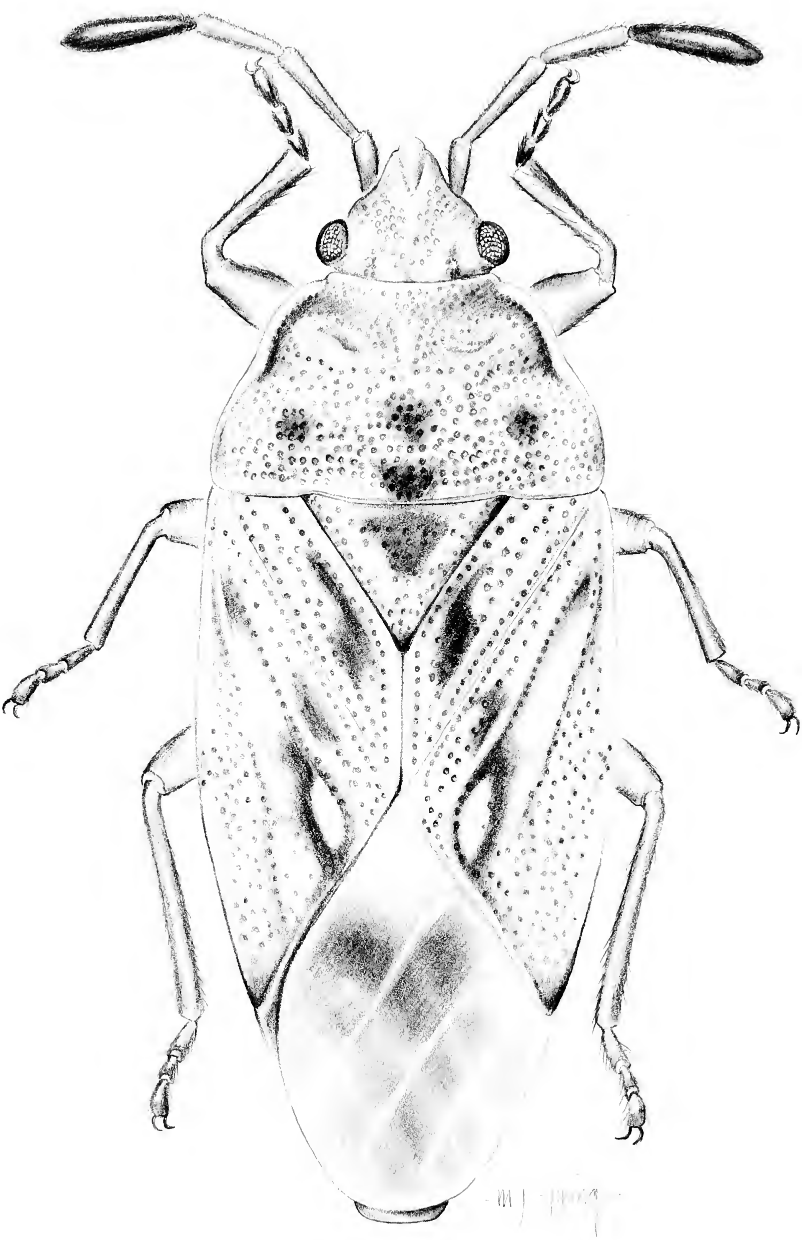
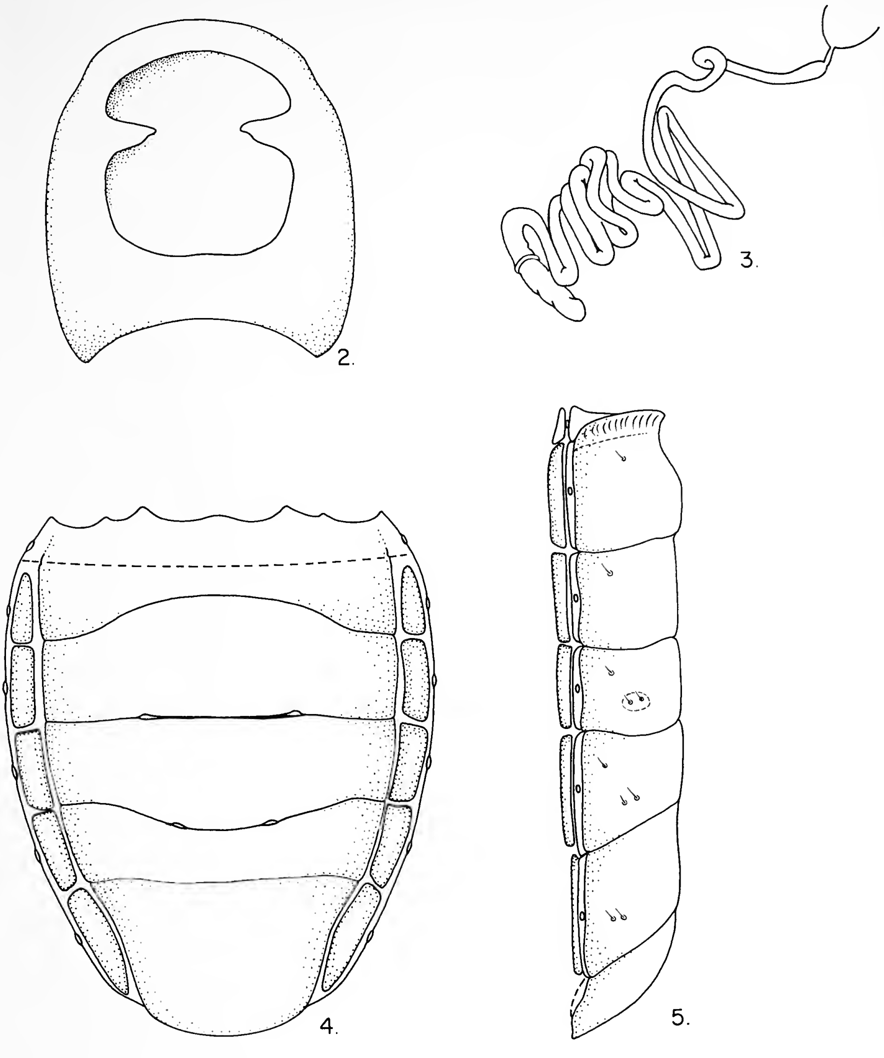


Fig. 1. *Polychisme ferruginosus* Stål, dorsal view.



Figs. 2–5. *Polychisme ferruginosus* Stål. 2. Genital capsule, dorsal view. 3. Spermatheca. 4. Abdomen, dorsal view. 5. Abdomen, lateral view.

Head non-declivent, tylus attaining middle of first antennal segment. Length head 0.64, width 0.72; interocular space 0.44. Pronotal surface irregular, transverse impression interrupted slightly mesad of midway between meson and margin by an elevated calloused area "connecting" calli with posterior lobe. Anterior collar broad, elevated with 2 to 2½ rows of large punctures. Lateral margins deeply sinuate, distinctly explanate throughout. Posterior margin very slightly convex. Length pronotum 0.80, width pronotum 1.44. Scutellum lacking a median ridge, but with a Y-shaped calloused yellow elevation. Length scutellum 0.60, width scutellum 0.74. Clavus broad with four distinct rows of punctures. Length claval commissure 0.54. Lateral corial margins slightly and evenly convex, broadly explanate. Apical corial margin slightly concave on distal two-thirds. Midline distance apex clavus-apex corium 0.86. Midline distance apex corium-apex membrane 0.72. Metathoracic scent gland auricle straight, moderately elongate, slightly angled dorso-ventrad. Evaporative area occupying most of mesopleuron. Fore femora moderately incrassate, mutic. Labium extending posteriorly almost to posterior margin of mesocoxae, first segment attaining base of head. Length labial segments I 0.40, II 0.40, III 0.34, IV 0.26. Antennal segments I, II, III terete, segment IV broader and fusiform. Length antennal segments I 0.26, II 0.44, III 0.28, IV 0.50. Total body length 3.92.

Described from a male from Colombia: Bucaramanga, 2,500 meters, Santander, 25.IV.1984 (Bordon).

Discussion. There is considerable color variation in the series before us, some specimens differ from the specimen described above in being almost entirely reddish yellow with dark color present only as claval maculae and the fourth antennal segment. The head and pronotal calli may be bright red contrasting with the anterior collar, a complete median stripe and fainter but still complete meso-lateral stripes and humeral angles of posterior pronotal lobe which are chocolate brown. Actually, although the specimen we describe above is vividly marked, it is the only specimen in the study series that has a dark third antennal segment; all other specimens have antennal segments I, II, III uniformly reddish or yellowish, contrasting with the dark fourth segment.

Despite the marked color variation, there is very little structural variation other than that found in a single male from "Cerro Oroque, Santander del Norte, Colombia." This specimen is either aberrant or more likely represents a different species. The anterior lobe of the pronotum has a conspicuous central elevation that extends well onto the posterior pronotal lobe, thus, confining the transverse impression to the lateral halves of the pronotum; the posterior pronotal lobe is somewhat rugulose, and the anterior collar less elevated. The corium has extensive dark striping posteriorly where it surrounds and forms two pale yellow macula adjacent to the apical corial margin. The genital capsule is as in Figure 2.

Material examined. Colombia: 2♂♂, Cund 2,900 m, Guasca, 10.III.1942 (Chapin). 1♂, locality as specimen described above. 1♂, 1♀, Roque, Santander del Norte, 8–9.VI.1965 (J. & B. Bechyne). 1♀, Mesa Rica, Santander del Norte, 30.V.1965 (J. & B. Bechyne). *Venezuela:* 2♂♂, Pmo. de Guaramacal, 3,200 m, BcCono Edo. Trujillo, 16.XI.1981 (Bordon). 1♂, Edo. Merida, El Valle, 2,400 m, 22.V.1983 (Bordon). 1♂, La Garita, 2,300 m, Tachira, 25.III.1984 (Bordon). 1♂, Toliferico, Merida, 3,500 m, 29.VI.1968 (J. & B. Bechyne). 1♂, 1♀, (in copulo), Rancho Grande, 1,800 m, 21.II.1967 (J. & B. Bechyne). 1♀, Pio Zmo (sp.?) la Negros, Tachira, 24.VI.1979 (B. Bechyne).

ACKNOWLEDGMENTS

We wish to extend our appreciation to Consejo Nacional de Ciencia y Tecnologia Mexico (CONACYT) and to Dr. Gonzalo Halffter for financial assistance to the junior author; to Ing. Carlos Bordon (Maracay, Venezuela) for the gift and loan of material; and to Ms. Mary Jane Spring and Mrs. Elizabeth Slater (University of Connecticut) for preparation of the illustrations and aid in the preparation of the manuscript, respectively. This work was supported in part by a grant to the senior author by the National Science Foundation.

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Received July 9, 1985; accepted October 25, 1985.

J. New York Entomol. Soc. 94(3):416–423, 1986

THREE NEW SPECIES OF *ACROSTERNUM* FIEBER, SUBGENUS *CHINAVIA* ORIAN, FROM MEXICO (HEMIPTERA: PENTATOMIDAE)

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Abstract.—Descriptions are provided for *Acrosternum* (*Chinavia*) *dubium,* new species; *A.* (*C.*) *solitum,* new species; and *A.* (*C.*) *triangulum,* new species, all occurring in Mexico. A key to all eight species of *Acrosternum* known to occur in Mexico is given.

Rolston (1983) recently revised the New World species of the genus *Acrosternum* Fieber, 1860, subgenus *Chinavia* Orian, 1965. Since this revision, three undescribed species from Mexico have been discovered. These are herein described, and a key is provided for the identification of the Mexican species of *Acrosternum.* Much of the following key was extracted from the key in the revision by Rolston (1983).

KEY TO MEXICAN SPECIES OF *Acrosternum*

1\. Abdominal spine projecting past anterior limit of metacoxae 2

– Abdominal spine or tubercle not surpassing metacoxae 3

2(1). No more than posterolateral angles of connexival segments black; abdominal spine conical, rounded in cross-section .... *froeschneri* Rolston

– Connexival spots large, each divided by transverse suture; abdominal spine compressed .... *scutellatum* (Distant)

3(1). Tibiae crimson proximally .... *montivagum* (Distant)

– Tibiae green or yellow proximally 4

4(3). Ventral surface of rostral segments 2–4 with mesial, black, longitudinal line broadly bordered on both sides with bright crimson .... *triangulum,* new species

– Ventral surface of rostral segments 2–4 with mesial, black, longitudinal line, but lacking crimson 5

5(4). Each spiracle surrounded by a distinct yellow spot; apex of scutellum usually pale yellow; distal one-fourth of antennal segment 3 usually green or fuscous, sometimes extreme distal end black .... *dubium,* new species

– Each spiracle at most surrounded by an obscure pale yellow spot; apex of scutellum green; distal one-fourth of antennal segment 3 usually black 6

6(5). Females 7

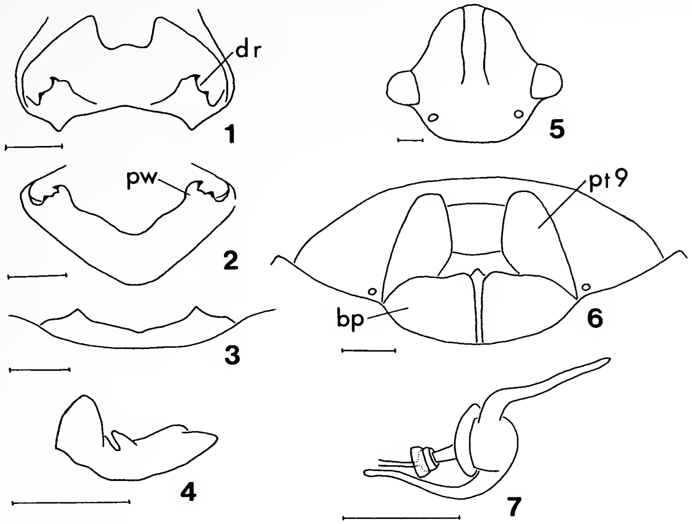
– Males 9

7(6). Posterior margin of basal plates evenly convex (Fig. 28) .... *hilare* (Say)

Each basal plate with posterolateral projection at base of 9th paratergite (Figs. 23, 32) 8

8(7). Projection of basal plate over paratergite clearly visible from ventral view (Fig. 22); from caudal view mesial margins of projection nearly parallel (Fig. 24) .... *solitum,* new species

– Projection of basal plate over paratergite only slightly visible from ventral view



Figs. 1–7. *A. triangulum*. 1. Genital cup, dorsal view; dorsal rim of posterior wall (dr). 2. Pygophore, caudal view; posterior wall (pw). 3. Pygophore, ventral view. 4. Paramere. 5. Head. 6. Genital plates, ventral view; basal plate (bp), 9th paratergite (pt 9). 7. Spermathecal bulb and pump. Dimensional lines equal 0.5 mm.

(Fig. 31); from caudal view mesial margins of projection divergent (Fig. 33) ....
.... *marginatum* (Palisot de Beauvois)

9(6). Posterior margin of pygophore from ventral view with broad shallow emargination (Fig. 27) .... *hilare* (Say)

– Posterior margin of pygophore from ventral view with deep, broadly V-shaped emargination (Figs. 19, 30) 10

10(9). Posterior margin of pygophore with small but distinct notch mesially from ventral view (Fig. 19) .... *solitum*, new species

– Posterior margin of pygophore without distinct small notch mesially from ventral view (Fig. 30) .... *marginatum* (Palisot de Beauvois)

Acrosternum (Chinavia) triangulum, new species

Figs. 1–7

Description. Medium green above with liberal amount of yellow or pale green on interstices between punctures except on head, green below blending to yellow mesially at least on thorax. Lateral dorsal and ventral margins of juga, pronotum, connexiva, and base of coria narrowly bordered by yellow or orange. Dorsal punctation dark green, dense on head and pronotum, less so on scutellum and coria. Length 11.4–14.6 mm.

Head evenly rounded apically; lateral margins of juga weakly concave, nowhere parallel (Fig. 5). Length of head 1.8–2.5 mm, width across eyes 2.8–3.2 mm. Antennae green except distal one-fourth of segment 3 and distal two-thirds of segments 4 and

5 sometimes fuscous or black; length of segments 1–5 about 0.4–0.5, 1.1–1.4, 1.3–1.6, 1.7–2.0, 1.6–1.8 mm.

Pronotum 6.8–9.0 mm wide at humeri, mesial length 2.2–2.8 mm. Humeral angle rounded, slightly produced beyond base of coria. Anterolateral margin of pronotum straight. No black on cicatrices.

Scutellum 4.1–5.5 mm wide at base, 5.0–6.3 mm long, with five spots equally spaced along base and often a vague mesial longitudinal line, pale yellow. No black on basal corners of scutellum. Corium rounded apically, reaching beyond middle of sixth (fifth visible) abdominal segment. Narrow lateral border of connexiva yellow or orange, interrupted by small black spot in each posterior angle, black spilling onto laterotergite.

Rostral segments 2–4 about 1.5–1.8, 1.1–1.3, 0.9–1.1 mm long, ventral surface with median black line bordered on both sides by crimson, apex of segment 4 piceous, terminating between metacoxae. Abdominal tubercle compressed, reaching to middle of metacoxae. Each ostiolar ruga extending about 0.8 distance from mesial margin of ostiole to lateral thoracic margin. Posterolateral angles of sternites black. Each spiracle pale brown to rufous, not located on callus, but sometimes surrounded by obscure yellow spot. Legs green.

Posterior margin of pygophore, from ventral view, with broad, shallow, slightly sinuous emargination with triangular projection on each side just mesad of lateral angles (Fig. 3); emargination sinuously U-shaped from caudal view (Fig. 2). Dorsal rim of posterior wall of genital cup diagonal, with 2 black teeth, the largest located at mesial corner of rim (Fig. 1). Paramere as in Figure 4. Posterior margin of basal plate slightly prominent mesially, slightly concave for mesial half, arcuate laterally; mesial margin of basal plate nearly straight (Fig. 6). Spermathecal bulb as in Figure 7.

Distribution. Southern Mexico.

Holotype. ♂, labeled "MEX: Yucatan, 1 km S. Xcalacoop, VI-11-1983, Coll. E. G. Riley." Deposited in the National Museum of Natural History, Washington, D.C.

Paratypes. 5♀♀, 7♂♂, labeled as holotype; 3♀♀, 3♂♂, labeled "MEX: Quintana Roo, 20 km N. Felipe Carrillo Puerto: VI-12-14-83: Coll. E. Riley"; 2♀♀, 1♂, labeled "MEX: Yucatan, Chichen Itza, VI-10-11-83, E. Riley"; 1♂, labeled "MEXICO: Oaxaca, 2.7 mi nw. El Cameron, July 24, 1973, Taken at light, Mastro & Schaffner."

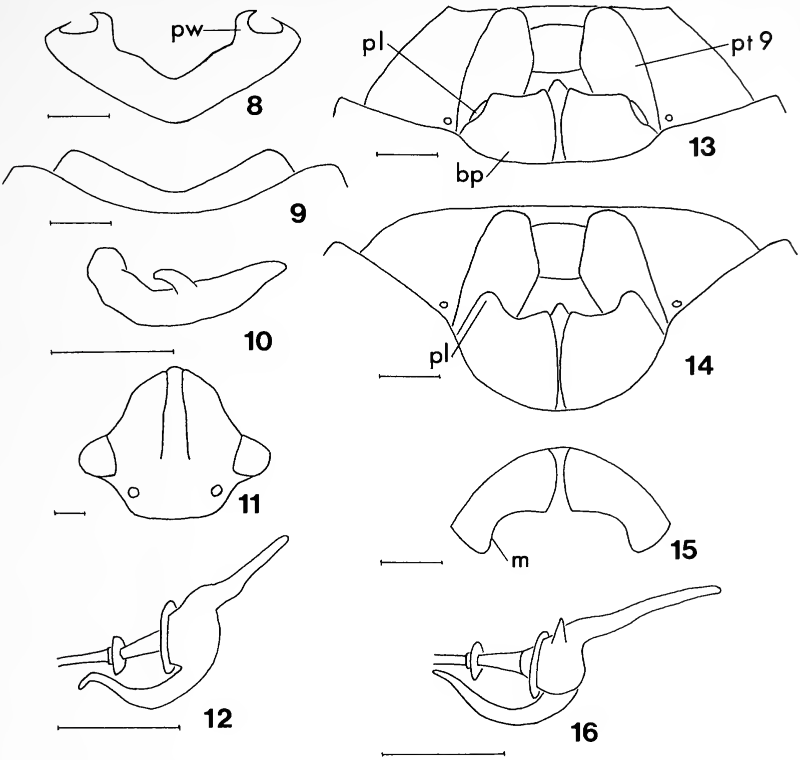
Comments. In the revision by Rolston (1983), this species keys to *A. hilare* (Say) from which it can be distinguished by the bright crimson on the ventral surface of the rostrum as well as by the genitalia. This species is named for the distinctive triangular projections on the posterior margin of the pygophore.

Acrosternum (Chinavia) dubium, new species

Figs. 8–16

Description. Medium green above, some yellow on interstices between punctures of scutellum, pale green below blending to pale yellow mesially. Lateral dorsal and ventral margins of juga, pronotum, connexiva, and bases of coria orange to orange-red. Dorsal punctation dark green. Length 12.0–15.0 mm.

Head evenly rounded apically, jugal margins concave, nowhere parallel (Fig. 11). Length of head 2.3–2.5 mm, width across eyes 2.9–3.3 mm. Each antenna green



Figs. 8–16. *A. dubium.* 8. Pygophore, caudal view; posterior wall (pw). 9. Pygophore, ventral view. 10. Paramere. 11. Head. 12. Spermathecal bulb and pump. 13. Genital plates, ventral view; basal plate (bp), posterolateral projection of basal plate (pl), 9th paratergite (pt 9). 14. Genital plates, caudoventral view; posterolateral projection of basal plate (pl). 15. Basal plates, caudal view; mesial margin of posterolateral projection (m). 16. Abnormal spermathecal bulb. Dimensional lines equal 0.5 mm.

except distal end of segments 3 and 4 and distal half of segment 5 sometimes fuscous; length of segments 1–5 about 0.5–0.6, 1.0–1.2, 1.2–1.5, 1.7–1.9, 1.7–1.8 mm.

Pronotum 6.9–8.6 mm wide across humeri, mesial length 2.4–2.9 mm. Humeral angle broadly rounded, not or scarcely produced beyond base of corium; anterolateral margin of pronotum straight. No black on cicatrices.

Scutellum 4.4–5.4 mm wide at base, 5.0–6.5 mm long, with five white spots equally spaced along base; apex usually pale yellow. No black on basal corners of scutellum. Coria rounded apically, reaching to or nearly to posterior edge of sixth (fifth visible) abdominal segment. Connexiva narrowly exposed, posterior angles black, spilling slightly onto laterotergites.

Rostral segments 2–4 about 1.5–1.8, 1.2–1.4, 1.1–1.2 mm long, pale brown, apex of segment 4 piceous, terminating between metacoxae. Abdominal spine compressed, reaching nearly to middle of metacoxae. Each ostiolar ruga reaching about 0.7 distance from mesial margin of ostiole to lateral thoracic margin. Posterolateral angles of sternites black. Each spiracle pale, not located on callus, but usually distinctly surrounded by yellow spot. Legs green, except proximal ends of tibiae usually yellow.

Posterior margin of pygophore, from ventral view, with V-shaped emargination, sides straight, not sinuous (Fig. 9); from caudal view, emargination sinuously U-shaped, with mesial margin of posterior wall nearly vertical (Fig. 8). Dorsal rim of posterior wall diagonal with tubercle in mesial corner of rim. Paramere as in Figure 10. Each basal plate with posterolateral projection over 9th paratergite (Fig. 14); this projection only slightly visible from ventral view (Fig. 13); mesial margin of posterolateral projection from caudal view broadly concave (Fig. 15); posteromesial corner of each basal plate slightly prominent (Fig. 14). Spermathecal bulb as in Figure 12.

Distribution. Revillagigedo Islands, Mexico.

Holotype. ♂, labeled (a) "Socorro Id., 2,000 ft, May 9, 1925" and (b) "H. H. Keifer Collector." Deposited in the California Academy of Sciences.

Paratypes. 3♀♀, labeled as holotype, except 1♀, "May 8 1925."

Comments. This species is closely allied to *A.* (*C.*) *marginatum* (Palisot de Beauvois), to which it keys in the revision by Rolston (1983). It can usually be distinguished from *A. marginatum* by the distinct yellow spot surrounding each spiracle, the pale yellow on the apex of the scutellum, and the decreased amount of black on antennal segment 3. The genitalia of both sexes also separate these species. In *A. dubium* the posterior margin of the pygophore from ventral view is V-shaped, with sides not at all sinuous. In *A. marginatum,* from ventral view, the posterior margin of the pygophore is usually sinuously V-shaped; however, in some specimens it is only slightly sinuate and appears very similar to *A. dubium.* The differences in the female genitalia are subtle but distinct. One female had an anomalous condition consisting of a triverticulate spermathecal bulb, the third projection being quite short (Fig. 16).

Acrosternum (Chinavia) solitum, new species

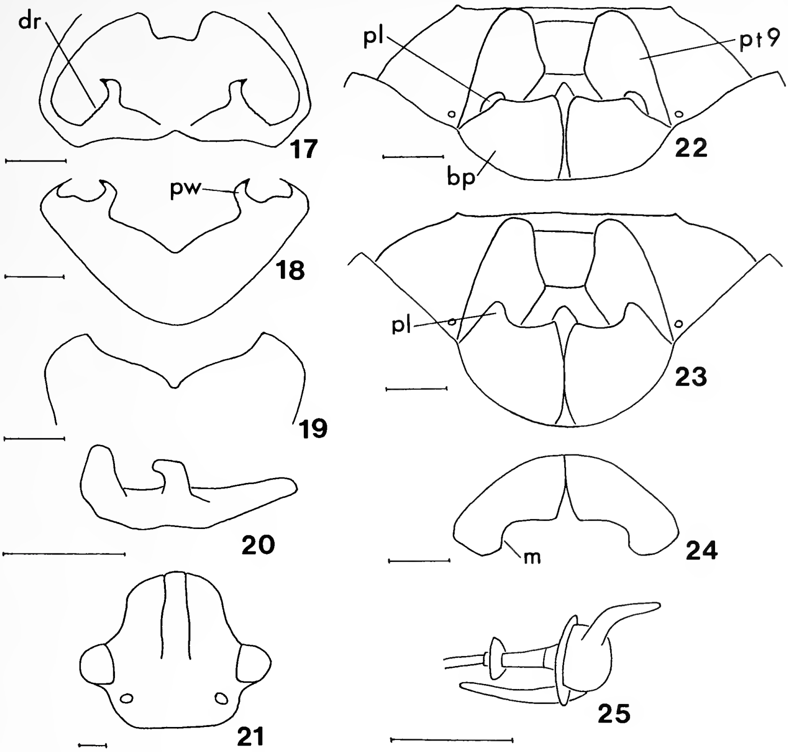
Figs. 17–25

Description. Medium to dark green above, green below becoming paler mesially. Lateral dorsal and ventral margins of juga, pronotum, connexiva, and bases of coria bordered with orange. Dorsal punctation dark green, dense on head, nearly rugose on pronotum, not so dense on scutellum and coria. Length 12.5–15.5 mm.

Head evenly rounded apically, jugal margins slightly concave before eyes, nowhere parallel (Fig. 21). Length of head 2.4–2.8 mm, width across eyes 3.0–3.5 mm. Each antenna green, rarely brown, except distal one-fourth of segment 3 black, distal one-third of segment 4 and distal half of segment 5 sometimes fuscous; length of segments 1–5 about 0.5–0.6, 1.1–1.4, 1.6–1.8, 1.9–2.3, 1.8–2.1 mm.

Pronotum 7.6–9.0 mm wide at humeri, mesial length 2.3–2.9 mm. Humeral angles rounded, slightly produced beyond base of coria. Anterolateral margin of pronotum straight or slightly convex. No black on cicatrices.

Scutellum 4.8–5.8 mm wide at base, 5.1–6.7 mm long, often with five pale yellow spots equally spaced along base of scutellum; some yellow on interstices between punctures of scutellum. No black on anterolateral corners of scutellum. Coria rounded

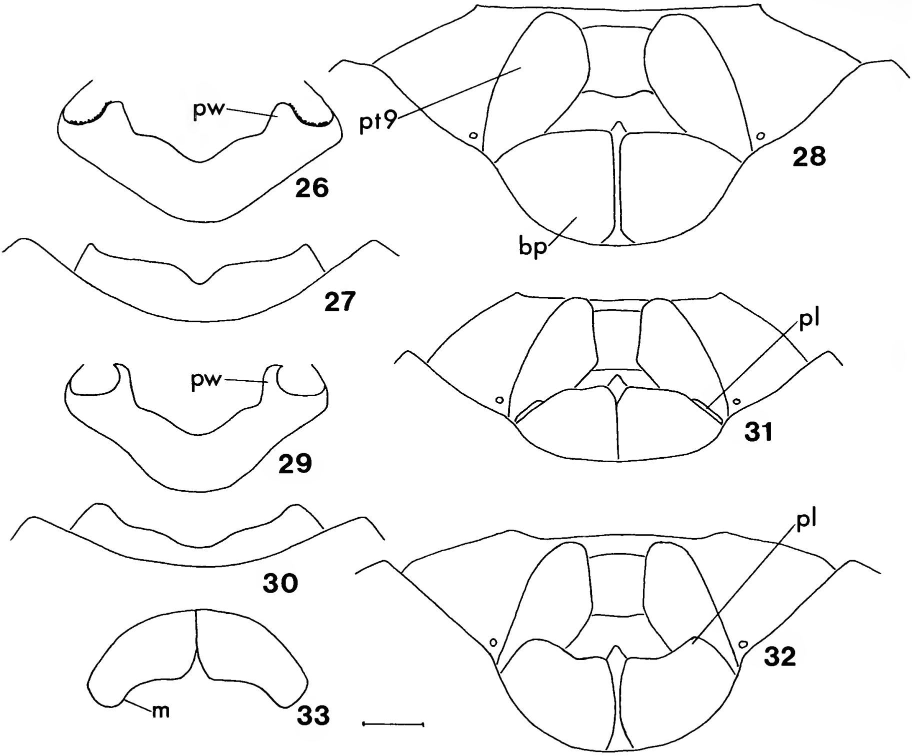


Figs. 17–25. *A. solitum.* 17. Genital cup, dorsal view; dorsal rim of posterior wall (dr). 18. Pygophore, caudal view; posterior wall (pw). 19. Pygophore, ventral view. 20. Paramere. 21. Head. 22. Genital plates, ventral view; basal plate (bp), posterolateral projection of basal plate (pl), 9th paratergite (pt 9). 23. Genital plates, caudoventral view; posterolateral projection of basal plate (pl). 24. Basal plates, caudal view; mesial margin of posterolateral projection (m). 25. Spermathecal bulb and pump. Dimensional lines equal 0.5 mm.

apically, reaching beyond middle of sixth (fifth visible) abdominal segment. Connexiva with posterolateral angles black, spilling onto laterotergites.

Rostral segments 2–4 about 1.6–1.9, 1.3–1.5, 1.1–1.3 mm long, pale green to brown, apex of segment 4 piceous, terminating between metacoxae. Each ostiolar ruga about three-fourths distance from mesial margin of ostiole to lateral thoracic margin. Abdominal spine compressed, reaching to middle of metacoxae. Posterolateral angles of sternites black. Each spiracle pale fuscous, not on callus, rarely surrounded by pale green spot. Legs green or brown.

Posterior margin of pygophore from ventral view broad, deep, slightly sinuate, V-shaped with small, distinct notch mesially (Fig. 19); emargination sinuously U-shaped from caudal view, with mesial margins of posterior wall convergent dorsally (Fig. 18). Dorsal rim of posterior wall diagonal with large black tooth at mesial corner



Figs. 26–33. 26–28. *A. hilare*. 26. Pygophore, caudal view; posterior wall (pw). 27. Pygophore, ventral view. 28. Genital plates, caudoventral view; basal plate (bp), 9th paratergite (pt 9). 29–33. *A. marginatum*. 29. Pygophore, caudal view; posterior wall (pw). 30. Pygophore, ventral view. 31. Genital plates, ventral view; posterolateral projection of basal plate (pl). 32. Genital plates, caudoventral view; posterolateral projection of basal plate (pl). 33. Basal plates, caudal view; mesial margin of posterolateral projection (m). Dimensional line equals 0.5 mm.

(Fig. 17). Paramere as in Figure 20. Each basal plate with posterolateral projection over 9th paratergite, clearly visible from ventral view (Fig. 22); mesial margins of posterolateral projection from caudal view nearly parallel (Fig. 24); posteromesial corners of basal plates prominent, often angulate (Fig. 23). Spermathecal bulb as in Figure 25.

Distribution. Central Mexico.

Holotype. ♂, labeled "MEXICO, Hgo., 3,400′, Minera Autlan (Otongo), 31 July 1982, C. W. & L. O'Brien & G. Wibmer." Deposited in the National Museum of Natural History, Washington, D.C.

Paratypes. 3♀♀, labeled as holotype; 1♀, labeled "MEX: Jal., 4 mi S. El Tuito, 1,200′, Hwy. 200, Aug. 10, 82: C. W. & L. O'Brien & G. W. Wibmer"; 1♀, labeled "MEXICO, SLP, Hwy. 85, 8 mi N. Tamazunchale, 700′, 24 July 1982, C. W. & L.

O'Brien & G. Wibmer"; 1♀, labeled "MEXICO: Tamaulipas, Bocatoma—6 mi S. of Gomez Farias, 19–23 May 1979, Marlin E. Rice coll."

Comments. This species also keys to *A.* (*C.*) *marginatum* (Palisot de Beauvois) in the revision by Rolston (1983), and is obviously closely related to that species. It can be distinguished from *A. marginatum* by the characters of the genitalia of both sexes. The small mesial notch in the posterior margin of the pygophore of *A. solitum* is not present in *A. marginatum.* Females of *A. solitum* have a proportionately longer posterolateral projection on each basal plate, which is clearly visible from ventral view. In *A. marginatum* this posterolateral projection is only slightly visible from ventral view.

ACKNOWLEDGMENTS

We would like to thank Paul H. Arnaud, Jr. (California Academy of Sciences) and Donald B. Thomas, Jr. (USDA-ARS Screwworm Research, Weslaco, Texas) for the loan of specimens for this study. We would also like to thank Joan B. Chapin (Louisiana State University) for reviewing the manuscript.

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Received April 3, 1985; accepted July 29, 1985.

J. New York Entomol. Soc. 94(3):424–433, 1986

THE GENUS *CYPTOCEPHALA* BERG, 1883 (HEMIPTERA: PENTATOMIDAE)

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Abstract.—*Cyptocephala alvarengai* and *C. pallida,* new species, are described. Diagnoses for other species are provided. *Thyanta elegantula* Jensen-Haarup, 1928, is placed in the synonymy of *Cyptocephala cogitabunda* Berg, 1883.

Berg (1883) proposed the genus *Cyptocephala* for a small, uncommon and previously unknown pentatomid, *C. cogitabunda.* The genus remained monotypic until Rolston and McDonald (1984) transferred four nominal species from *Thyanta* Stål to *Cyptocephala.* These species were described originally as *Pentatoma antiguensis* Westwood, 1837, *Thyanta bimini* Ruckes, 1952, *Thyanta elegans* Malloch, 1919, and *Thyanta* (*Parathyanta*) *elegantula* Jensen-Haarup, 1928. Two new species are now added to the genus and *C. elegantula* is placed in the synonymy of *C. cogitabunda.* A key is provided to aid in the recognition of the species.

Cyptocephala, Berg, 1883

Cyptocephala Berg, 1883:209–210 (reprinted 1884:25–26); Rolston and McDonald, 1984:74–77.
Crato Distant, 1893:457. (Synonymized by Rolston, 1976.)
Thyanta subgenus *Parathyanta* Jensen-Haarup, 1928:186. (Synonymized by Rolston and McDonald, 1984.)
Thyanta (in part): Rolston, 1972:282, 284–285; Rolston 1976:6.

Diagnosis. Juga projecting little if any beyond tylus, apex of head either shallowly emarginated or smoothly convex. Bucculae arcuately truncate posteriorly; first rostral segment lying entirely between them; rostral apex reaching to or slightly beyond base of abdomen. Ocelli lying entirely behind imaginary line drawn across posterior limit of reticulation of eyes. Interocular width more than one-half width of head across eyes. Anterolateral margin of pronotum angular dorsoventrally, at least posteriorly, sometimes narrowly reflexed posteriorly, without rim, entire; anterior margins of propleura not produced. Scutellar width at distal end of frena 0.30–0.45 basal width. Ostiolar juga on each side extending 0.7–0.80 distance from mesial margin of ostiole to lateral margin of metapleuron. Femora unarmed, tibiae sulcate. Costal angle of each corium lying above penultimate segment. Abdominal venter without basal tubercle or spine.

Parameres bilobed with fine denticles between lobes. Dilation of spermathecal duct not extending full length of enclosed sclerotized rod; enlargement usually present proximad of proximal flange. Spiracles present on 8th paratergites.

Type-species. The type species of *Cyptocephala* is *Cyptocephala cogitabunda* Berg, 1883, by monotypy; that of *Crato* is *Crato urbicus* Distant, 1893, by monotypy = *Cyptocephala antiguensis* (Westwood, 1837); and that of *Thyanta* subgenus *Parathyanta* Jensen-Haarup, 1928, is *Thyanta* (*Parathyanta*) *elegantula* Jensen-Haarup 1928 by original designation = *Cyptocephala cogitabunda* Berg.

Comments. *Cyptocephala* is near *Thyanta* Stål and *Tepa* Rolston and McDonald, but it differs especially in having bilobed, denticulate parameres.

KEY TO SPECIES

1. Wide, white, calloused band on each side ventrally, beginning beneath eye and continuing across pleura with interruptions at anterior and posterior pleural margins .... *elegans* (Malloch)

– Venter lacking calloused band 2

2(1). Juga projecting slightly past tylus, producing shallow emargination in apex of head .... *cogitabunda* Berg

– Apex of head smoothly arcuate 3

3(2). Anterior lobe of parameres acute apically (Fig. 1); maximum length of each 9th paratergite less than twice its maximum width (Fig. 15) ...... *alvarengai*, new species

– Anterior lobe of parameres narrowly to broadly rounded; maximum length of each 9th paratergite about 2.5 times its maximum width 4

4(3). Females 5

– Males 7

5(4). Basal plates tumescent, from lateral view disc protruding beyond mesial margin of plates at base .... *antiguensis* (Westwood)

– Basal plates convex but not tumescent, disc not protruding beyond mesial margin of plates at base 6

6(5). Minimal distance between 9th paratergites 1.5–2.0 times length of 10th sternite (Fig. 16); basal plates somewhat umbonate in apical angle; last two segments of antennae without apical bands .... *bimini* (Ruckes)

– Minimal distance between 9th paratergites 1.2–1.3 times length of 10th sternite (Fig. 17); basal plates lacking umbo; last three segments of antennae bicolored, pale green to cream basally, rufous to light brown distally .... *pallida*, new species

7(4). Ventral margin of parameres foliate (Fig. 7) .... *bimini* Ruckes

– Ventral margin of parameres not expanded 8

8(7). Width of scutellum at end of frena less than ⅖ of basal width; carina entad of parameres on each lateral wall of genital cup at least partially visible (Fig. 4) .... *pallida*, new species

– Width of scutellum at end of frena ⅖ or more of basal width; denticle entad of parameres on each lateral wall of genital cup concealed by parameres .... *antiguensis* (Westwood)

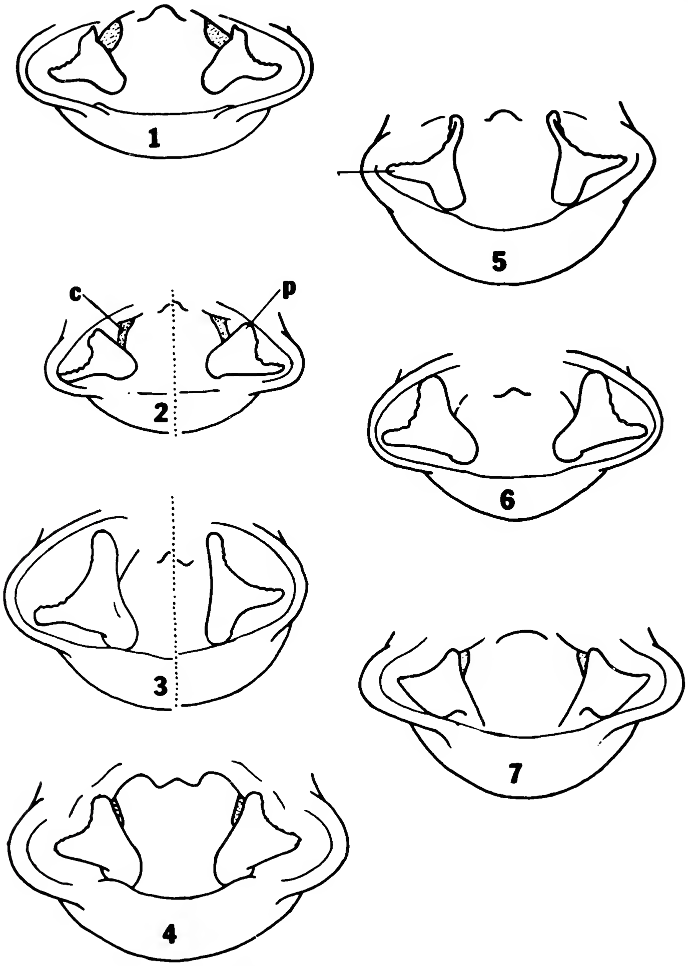
Cyptocephala elegans (Malloch)

Figs. 5, 12

Thyanta elegans Malloch, 1919:217, 218, figs. 71, 76, 77; Rolston, 1972:284, figs. 52–58.

Cyptocephala elegans: Rolston and McDonald, 1984:77, figs. 39, 41.

Diagnosis. Wide, calloused white band on each side ventrally, beginning beneath eye and continuing across pleura with interruptions at anterior and posterior pleural margins. Dorsum green with multihued, variable markings; head flavescent excepting



Figs. 1–7. Genital cup. 1. *C. alvarengai.* 2. *C. cogitabunda,* variation in parameres. 3. *C. antiguensis* from Dominican Republic (left) and Grenada (right). 4. *C. pallida.* 5. *C. elegans.* 6. *C. antiguensis* from Mexico. 7. *C. bimini.* Symbols: carina (c); paramere (p).

apex, tylus and vertex green; humeri usually connected by irregular, ivory callus bordered with rufous; broad lateral border on scutellum, often exocoria and narrow border along anterolateral margins of pronotum, all white to flavescent with rufous punctures and a few fuscous punctures.

Lateral margins of juga tapering sinuously to evenly rounded apex of head, nowhere parallel; anteocular concavity shallow. Anterolateral margins of pronotum nearly straight, weakly reflexed near humeri. Width of scutellum at end of frena about 0.4 basal width. Length excluding hemelytral membranes 6.0–7.0 mm.

Parameres concealing denticle on each lateral wall of genital cup, abruptly bent, appearing trilobed in genital cup (Figs. 5, 12).

Distribution. Florida (Hillsborough, Monroe, Sarasota counties) and Texas (Aransas, Brazoria, Cameron, Kleburg, and Nueces counties along Gulf of Mexico).

Type. Not seen.

Comments. This rare, colorful species varies greatly in dorsal markings, but the calloused, pleural bands are apparently constant.

Cyptocephala cogitabunda Berg

Figs. 2, 9

Cyptocephala cogitabunda Berg, 1883:210–211; Berg, 1884:26–27 (reprint of Berg, 1883); Berg, 1891:282–283; Rolston and McDonald, 1984:77, fig. 38.
Thyanta elegantula Jensen-Haarup, 1928:186, 188, 191. **New Synonymy.**
Cyptocephala elegantula: Rolston and McDonald, 1984:77.

Diagnosis. Extremely variable in color and markings, ranging in predominant color from dark brown to dark green. Scutellum usually with pale mesial band beginning most often caudad of basal disc and continuing to apex, this band often bordered subapicallly with elongated patch of dark castaneus to fuscous punctures. Pale, transhumeral band often present, limited posteriorly by narrow, irregular callus; latter sometimes bordered posteriorly by narrow band of rufous to fuscous punctures. Exocoria often pale, at least basally.

Juga projecting slightly beyond tylus, causing shallow emargination in apex of head, their lateral margins briefly parallel or subparallel before rather shallow anterocular concavity. Anterolateral margins of pronotum concave, somewhat reflexed at humeri. Humeri subangular, projecting laterad of corresponding corium by 0.4–0.8 width of eye. Scutellar width at end of frena 0.38–0.44 basal width. Pleura uncalloused. Size extremely variable, 4.8–7.7 mm long excluding hemelytral membranes.

Carina on each side of genital cup mostly visible entad of parameres (Fig. 2). Lateral lobe of parameres narrow; anterior lobe wider, usually moderately rounded apically, sometimes irregular from denticulation (Figs. 2, 9).

Distribution. Argentina (Buenos Aires, Catamarca, Córdoba, Mendoza, San Luis, Tucumán); Bolivia (La Paz); Uruguay (Colonia). The northern range is considerably greater if a specimen purportedly from Lima, Peru, is correctly labeled.

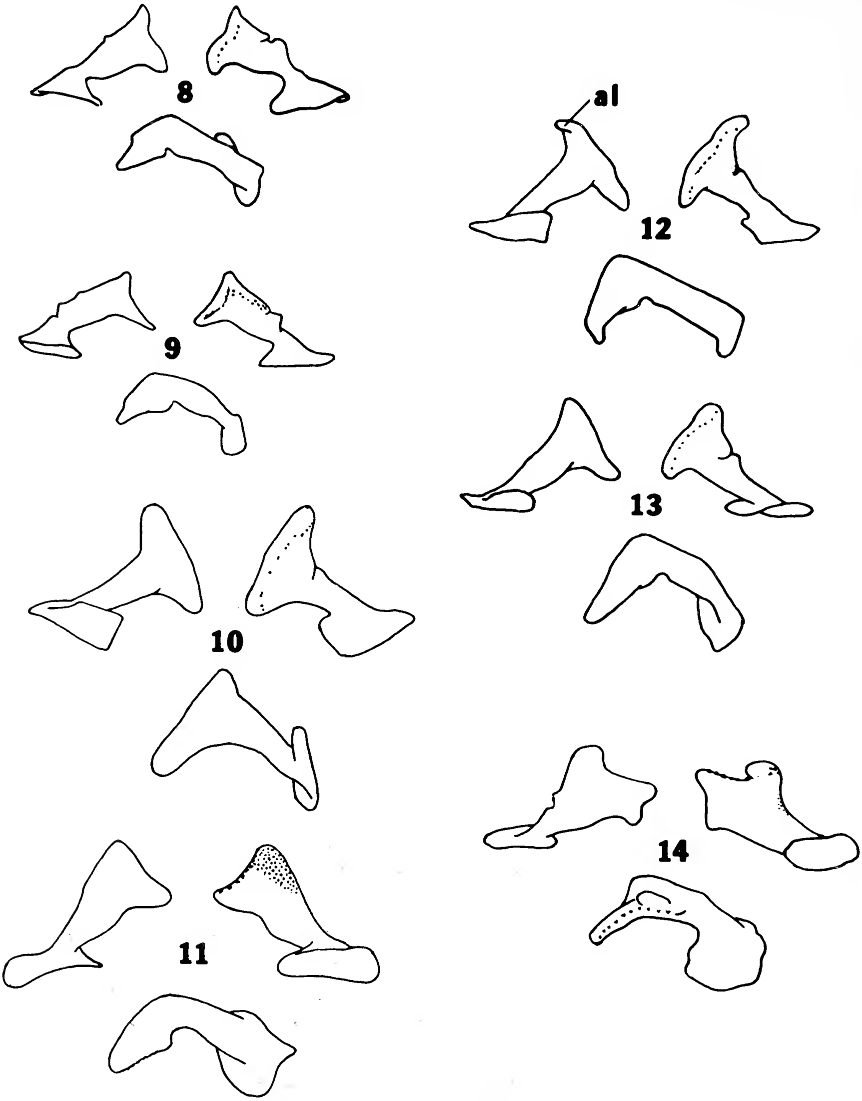
Types. Dr. Jocélia Grazia compared a female specimen sent to her with the holotype of *C. cogitabunda,* a female, and judged the two specimens to be conspecific. The holotype *Thyanta elegantula,* a male, was examined.

Comments. C. cogitabunda is the only species in the genus in which the juga are longer than the tylus, thus creating a shallow emargination in the apex of the head. It is also the only one with distinctly concave anterolateral pronotal margins; in the other species these margins are weakly concave or straight.

Cyptocephala alvarengai, new species

Figs. 1, 8, 15, 18–20

Description. Light tan or pale green, usually with variable, vague patterns of fuscous and/or rufous punctures; some light green individuals conspicuously marked with much of head, a broad band connecting humeri, and apical part of scutellum rufous



Figs. 8–14. Right paramere, ectal view (upper left), ental view (upper right), mesial view (lower). 8. *C. alvarengai.* 9. *C. cogitabunda.* 10. *C. antiguensis* from Dominican Republic. 11. *C. pallida.* 12. *C. elegans.* 13. *C. antiguensis* from Mexico. 14. *C. bimini.* Symbol: anterior lobe (al).

or rufously punctate; densely punctate spot on apex of scutellum fuscous or castaneous, occasionally reduced to a few punctures. Length excluding hemelytral membrane 5.2–8.3 mm.

Lateral margins of juga parallel or subparallel between anteocular concavity and smoothly arcuate apex of head. Antennae dark stramineous or light green, apical ½ or less of segment 3 and all of segments 4 and 5 brown, castaneous or rufous; length of segments 0.3–0.4, 0.6–0.9, 0.75–1.0, 0.8–1.0, 0.85–1.0 mm. Rostral segments 2–4 about 1.1–1.5, 0.6–0.8, 0.6–0.8 mm in length; last segment mostly black, reaching from posterior margin of metacoxae to posterior margin of sternite 3 (2nd visible). Width of head across eyes 1.5–2.0 mm, mesial length 1.4–1.8 mm; interocular width 0.95–1.20 mm; distance across ocelli 0.85–1.05 mm.

Anterolateral margins of pronotum weakly concave. Interstices between punctures often calloused between humeri, forming narrow, irregular band. Width of pronotum at humeri 3.3–4.7 mm, mesial length 1.3–1.9 mm.

Mesial stripe with few or no punctures often present on scutellum distally, ending at small, marginal cluster of fuscous or castaneous punctures. Basal width of scutellum 2.0–3.2 mm, length 2.1–3.1 mm; width at distal end of frena 0.36–0.42 of basal width. Coria rather uniformly punctate; membranes hyaline, or with mesial veins brown, or with prominent mesial vitta. Connexiva little or not at all exposed, immaculate or sordid to fuscous, usually with marginal, semicircular, pale macule.

Ventral punctation usually castaneous to fuscous with black dot at base of mesial trichobothrium of each pair. Lateral angles of sternites usually minutely marked with black.

Greatest width of each 9th paratergite nearly ½ its greatest length (Fig. 15). Basal plates convex but not tumescent, without umbo.

Anterior lobe of parameres terminating in acute cone, occasionally spinose; lateral lobe subacute or narrowly rounded apically (Figs. 1, 8). Aedeagus as in Figures 19, 20.

Distribution. Northeastern Brazil, states of Bahia, Ceara, Minas Gerais and Pernambuco.

Holotype. ♂, labeled "Brazil: Pernambuco State, Petrolina, V-1969. M. Alvarenga." Deposited in Museu Nacional, Rio de Janeiro.

Paratypes. Labeled as holotype (39♂♂, 41♀♀); "Brazil: Ceara State, Crato, 850 m, Serra do Araripe. V-1969, M. Alvarenga" (3♂♂, 1♀); "Brazil, Bahia: Encruzilhada, 960 m, Nov. 1972, N. Alvarenga" (1♂, 1♀); "Independencia, Brazil, Mann" (2♂♂); "Cordisburgo, Minaes Gerais, BRAZIL, 7–8 Nov. 19-Cornell University Expedit, Cornell U. Lot 569 Sub 84" (1♀).

Comments. The range of this species is not known at present to overlap that of any other spsecies of the genus. Of the other two congeners in South America, the known range of *cogitabunda* is considerably to the south and west, and the range of *antiguensis* apparently does not extend southward into that of *alvarengai.*

Etymology. This species is named for Moacir Alvarenga, one of the few recent and major collectors of South American insects.

Cyptocephala antiguensis (Westwood)

Figs. 3, 6, 10, 13

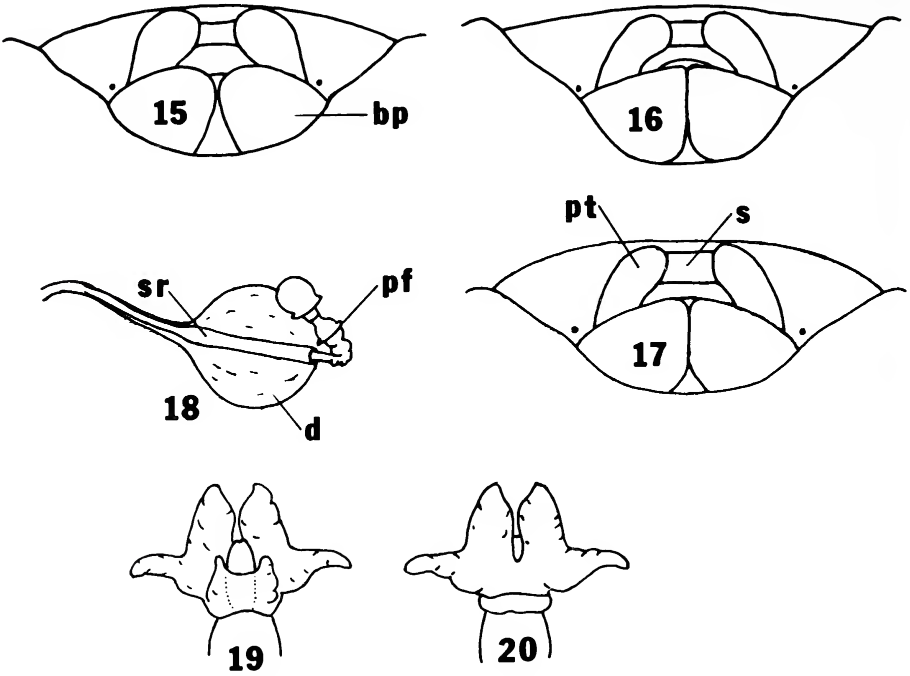
Pentatoma antiguensis Westwood, 1837:36

Pentatoma taeniola Dallas, 1851:250–251. (Synonymized by Distant, 1900.)

Thyanta taeniola: Stål, 1862:58; Distant, 1880:66, pl. 7, fig. 4.

Crato urbicus Distant, 1893:457, pl. 39, fig. 22. (Synonymized by Rolston, 1976.)

Thyanta antiguensis: Distant, 1900:812; Rolston, 1972:281–282, figs. 43–51; Rolston, 1976:4, 6.



Figs. 15–20. Genital plates. 15. *C. alvarengai.* 16. *C. bimini.* 17. *C. pallida.* 18. Spermatheca, *C. alvarengai.* 19. Distal part of aedeagus, *C. alvarengai,* dorsal view. 20. Same, ventral view. Symbols: basal plates (bp), dilation of spermathecal duct (d), paratergite 9 (pt), sclerotized rod (sr), sternite 10 (s), proximal flange (pf).

Thyanta picturata Ruckes, 1957:42–44. (Synonymized by Rolston, 1972.)
Cyptocephala antiguensis: Rolston and McDonald, 1984:77, figs. 19, 36.

Diagnosis. Variable in color, ranging from uniform light tan to rich green with ivory, rufous and black markings, especially as multihued transhumeral band and macule on scutellar apex.

Lateral margins of juga parallel or subparallel between anteocular concavity and more or less evenly rounded apex of head; juga not surpassing tylus. Anterolateral margins of pronotum straight to weakly concave, not reflexed. Scutellar width at end of frena 0.38–0.46 of basal width. Pleura uncalloused. Length excluding hemelytral membrane 5.5–7.8 mm.

Basal plates tumescent, their mesial margins not visible at base from lateral view. Parameres concealing denticle on each lateral wall of genital cup: anterior lobe of each varying in width, equal to or much wider than width of lateral lobe (Figs. 3, 6, 10, 13).

Distribution. Ranging from southern California, Arizona, Texas and Florida through Middle America and the West Indies, across northern South America and as far south as northern Peru in the Andean region.

Comments. The tumescent basal plates of females are distinctive and unique within the genus; and only in this species and *elegans* do the parameres completely conceal the denticle or carina on each lateral wall of the genital cup. *Cyptocephala antiguensis* lacks the calloused pleural bands that are characteristic of *elegans.*

In the western range of this species, at least as far south as western Panama, the lobes of the parameres are quite unequal in width (Fig. 6). In the eastern range these lobes are subequal in width from Puerto Rico southward throughout the Lesser Antilles and South America (Fig. 3, right). However, the typical western form also occurs in Florida, Cuba, and Jamaica, and intermediates between the western and eastern forms occur in Florida, Cuba and Hispaniola (Fig. 3, left). Whether or not there is a comparable zone of intergration in eastern Panama and/or the contiguous part of Colombia is unknown, but most of the few males seen from western Panama do show a narrowing of the anterior lobe.

Cyptocephala bimini (Ruckes)
Figs. 7, 14, 16

Thyanta bimini Ruckes, 1952:65–67.
Cyptocephala bimini: Rolston and McDonald, 1984:77, figs. 21, 22, 37, 40.

Diagnosis: Antennal segments usually almost unicolorous, light green or tan; occasionally apex of segment 3 and last two segments dark green, rarely segments 4 and 5 with broad, subapical, light rufous band. Pronotum lacking fascia between humeri.

Lateral margins of juga tapering slightly between anteocular concavity and smoothly arcuate apex of head. Pronotum not distinctly depressed submarginally between humeri and cicatrices; anterolateral margins nearly straight, narrowly and weakly reflexed from humeri to cicatrices. Scutellar width at end of frena 0.30–0.38 of basal width. Pleura uncalloused. Length excluding hemelytral membranes 6.5–8.8 mm.

Minimal distance between 9th paratergites 1.5–2.0 times length of 10th sternite (Fig. 16). Disk of basal plates somewhat umbonate in mesial angle. Carina on each lateral wall of genital cup partially exposed entad of parameres. Ventral margin of parameres foliate (Figs. 7, 14).

Distribution. Bahama Islands (Cat Isl., Long Isl., Grand Bahama, Mayaguana Isl., New Providence Isl., Rum Cay, South Bimini Isl.), Cuba, Dominican Republic, Florida (Dade Co., Monroe Co.), Jamaica, and Puerto Rico.

Type. The holotype was examined.

Comments. Of congeneric, sympatric species, *C. bimini* most closely resembles *pallida.* Both sexes of these species are separable by the genitalia, and they also differ, although less decisively, in the color of the antennae, form of the head before the eyes, and contour of the anterolateral submargin of the pronotum.

Cyptocephala pallida, new species
Figs. 4, 11, 17

Description. Pale green to cream with darker punctures. Length excluding hemelytral membranes 7.2–8.5 mm.

Lateral margins of juga parallel between anteocular concavity and smoothly arcuate apex of head. Apex of antennal segment 3, distal ½ or more of 4, distal ¾ or more of 5, and sometimes tarsi faintly rufous or light brown; length of segments 0.4–0.45, 0.95–1.1, 0.8–1.05, 0.9–1.1, 0.9–1.05 mm. Rostral segments 2–4 about 1.1–1.3, 0.6–0.8, 0.7–0.8 mm long; apex projecting slightly past metacoxae. Width of head across eyes 1.8–2.1 mm, mesial length 1.5–1.9 mm; interocular width 1.1–1.3 mm; distance across ocelli 0.7–8.5 mm.

Anterolateral margins of pronotum nearly straight, slightly reflexed from humeri as far cephalad as cicatrices. Shallow but distinct submarginal depression located between each humerus and corresponding cicatrice; disk lacking fascia between humeri; punctation behind imaginary transhumeral line usually slightly stronger and sometimes darker than punctation before line. Pronotal width at humeri 4.1–4.7 mm, mesial length 1.5–1.8 mm.

Vague mesial stripe due to less dense punctation usually present on scutellum. Basal width of scutellum 2.6–3.3 mm, mesial length 2.7–3.5 mm; width at distal end of frena 0.32–0.36 of basal width. Small, scattered, subcalloused macules usually numerous on coria; hemelytral membranes hyaline, occasionally with a few inconspicuous, small, fumose spots along veins. Black dot on posterolateral corners of connexival segments not extending onto laterotergites.

Pleura rather uniformly punctate excepting nearly impunctate evaporative areas. Posterolateral angles of each sternite with small, black spot. Punctation on sternites moderately dense.

Minimal distance between 9th paratergites 1.2–1.3 times length of 10th sternite (Fig. 17). Basal plates convex but not tumescent, without umbo.

Anterior lobe of parameres wider than lateral lobe, broadly rounded, leaving carina on each lateral wall of genital cup at least partially visible (Fig. 4); ental face of anterior lobe with spiculate field (Fig. 11).

Distribution. Virgin Gorda Island (British Virgin Islands) and Hispaniola.

Holotype. ♂, labeled "Virgin Gorda BVI, Prickly Pear Id, Vixen Pt 14.IV.56, J. F. G. Clarke"; deposited in the National Museum of Natural History, Washington, D.C.

Paratypes. Labeled as holotype (3♀♀, NMNH); labeled as holotype except date "6-IV-1958" (♂); "Pt au Pr, Hayti, feb." (♂, UAT); "Dom. Rep., S. R. 9 km E Stgo, Rodriguez, May 28, 1978, CW & LB O'Brien and Marshall" (♂).

Comments. This species resembles *C. bimini* in size and color, and the two species are at least partially sympatric. They are separable by the genitalia of both sexes and also differ in antennal color, form of the head before the eyes, and contour of anterolateral submargin of the pronotum.

ACKNOWLEDGMENTS

I am grateful to the following individuals for their contributions to this study: N. Møller Andersen (Universitetets Zoologiske Museum, Copenhagen), W. R. Dolling (British Museum (Natural History)), H. Dodge Engleman, R. C. Froeschner (Smithsonian Institution), Jocélia Grazia (Universidade Federal do Rio Grande do Sul), M. W. R. de V. Graham and I. Lansbury (University Museum, Oxford), C. A. Olson (University of Arizona, Tucson), and Randall T. Schuh (American Museum of Natural History).

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Received March 1, 1985; accepted November 15, 1985.

J. New York Entomol. Soc. 94(3):434–441, 1986

NOTES ON THE GENUS *IOSCYTUS* WITH THE DESCRIPTION OF A NEW SPECIES AND KEY TO SPECIES (HEMIPTERA: HETEROPTERA: SALDIDAE)

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Abstract.—Recent collections of *Ioscytus* Reuter in the United States have revealed the first known member of the genus from the eastern United States, described here as *Ioscytus chapmani,* new species, and a new distributional record for the United States and first recorded submacropterous form for *Ioscytus tepidarius* (Hodgden), heretofore known only from Mexico. The various habitats of *Ioscytus* species are described, and a key to species and distributional map are included.

Several years ago while collecting in Ohio one of us (CNM) collected a series of an unusual saldid. This represented a great eastward expansion of the genus *Ioscytus* since no other species were known east of Colorado. Comparison with all described species showed this species to be new and it is described here. It possesses a type IIIA stridulatory mechanism (see Polhemus 1977, 1985), unique to the genus *Ioscytus.*

A series of *Ioscytus tepidarius* (Hodgden) was collected in Arizona, and as this species was previously known only from Mexico, this is a new record for the United States. The Arizona specimens differ from Mexican material examined in that they are submacropterous, therefore a description of this form is included. Also included are a key to the known species of *Ioscytus* and a distributional map to help spur an interest in the group. The habitat preferences of *Ioscytus* are unusual within the Saldidae, often species specific, and are discussed.

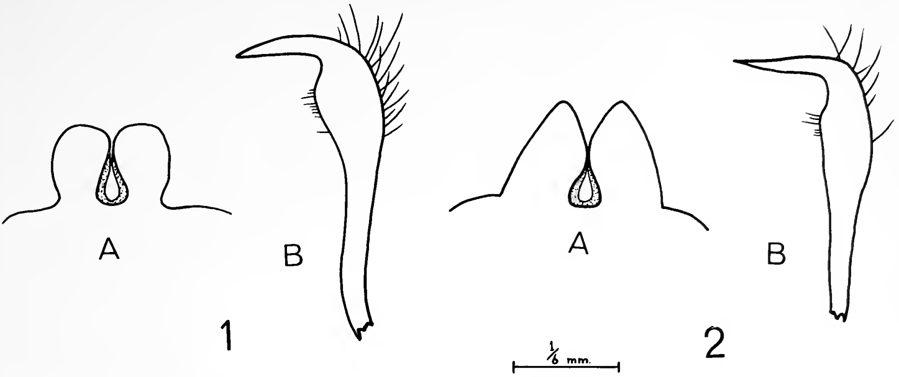
All specimens are in the collection of the authors (CNM and JTP), American Museum of Natural History (AMNH), U.S. National Museum (USNM) and Oregon State University (OSU). All measurements are in mm.

Ioscytus chapmani, new species
Figs. 2–4

Description. Male: Submacropterous, moderate in size, general color black, dorsum glabrous with long erect black setae, last antennal segment leucine except narrowly dark basally.

Head: Black, shining, anteclypeus, postclypeus black with numerous setae; long erect setae on frons and vertex; vertex slightly carinate between eyes. Ocelli round, separated by one and one-half times the width of an ocellus. Eyes reddish-brown, slightly longer than wide (0.60:0.43); rostrum light brown, surpassing the hind coxae.

Thorax: Pronotum black, shining, smooth, covered with long erect black setae; collar encircled with numerous small pits; callus strongly raised with a deep depression medially; lateral margins straight with numerous black setae at anterior margin; callus



Figs. 1, 2. 1. *Ioscytus tepidarius,* ♂: a. parandria (lateral view); b. right paramere (lateral view). 2. *Ioscytus chapmani,* ♂: a. parandria (lateral view); b. right paramere (lateral view).

posteriorly demarcated by a row of small pits; scutellum as wide as long (0.67:0.65), anterior portion raised, posteriorly faintly rugose; venter black, covered with short golden recumbent setae.

Wings: Hemelytra covered with long erect black setae, shining, embolium hyaline, extending to fracture of membrane; secondary hypocostal ridge with strigil; membrane with two closed cells, brown; corium and clavus similar in texture and color.

Extremities: Antennae dark brown except segment I and basal two thirds of segment II reddish flavous; segment IV except narrow dark basal part, luteous; segment II with long setae; third and fourth segments thicker than first two. Antennal measurements: I, 0.38; II, 0.85; III, 0.57; IV, 0.68. Legs reddish flavous.

Genital structures: Capsule small, black; parameres small, processus hamatus sharply pointed; corpus paramerus sparsely set with long setae; parandria angulate distally. See Figure 2a, b.

Measurements: Holotype (♂), length 3.50, width 1.70. Allotype (♀), length 3.84, width 1.97. Mean length of 10♂♂, 3.49, Std. Dev. 0.10. Mean width of 10♂♂, 1.72, Std. Dev. 0.06. Mean length of 10♀♀, 3.85, Std. Dev. 0.15. Mean width of 10♀♀, 1.99, Std. Dev. 0.10.

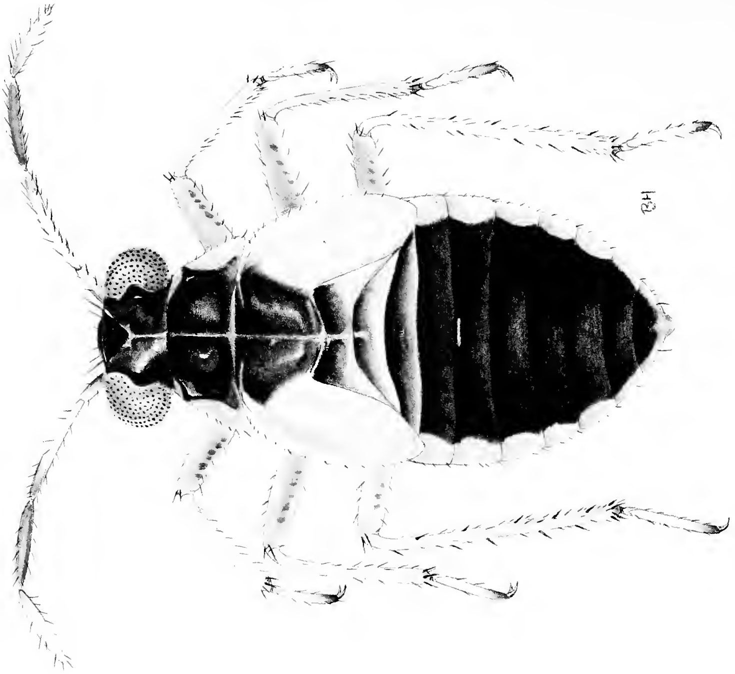
Female: Larger and more robust than male; coloration similar to male; see Figure 3a.

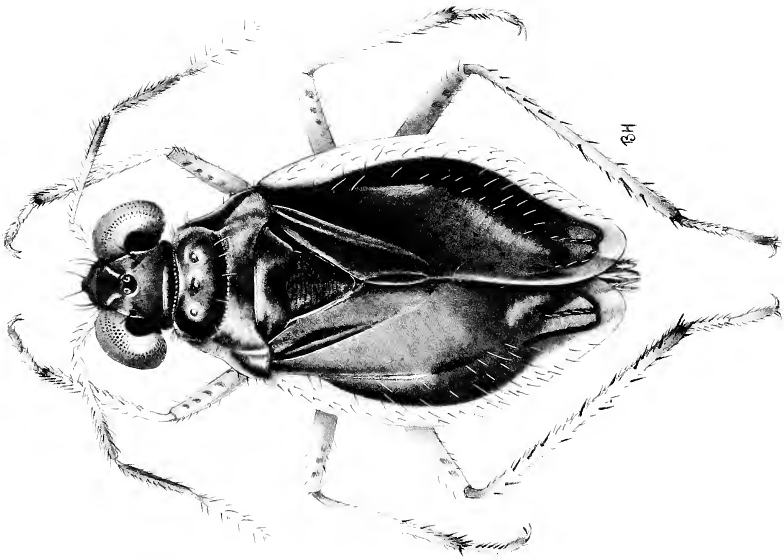
Immature: Last instar black; wing pads, connexivum and lateral margin of pronotum leucine; last antennal segment leucine except for dark narrow band basally, Figure 3b.

Holotype ♂ and allotype ♀. OHIO, Washington Co., Veto Lake State Park, IX. 6, 1981, C. N. McKinnon (holotype to be placed in USNM).

Paratypes. 21♂♂, 18♀♀, same data as types (CNM, JTP, AMNH). KENTUCKY (1♀, 1 nymph), Jessamine Co., Marble Creek, IX. 24, 1966, T. C. Barr (OSU). VIRGINIA (1♂), Montgomery Co., 5 mi SE Radford, Meadow Creek, Cty. Rt. 60, VI. 22, 1984, R. Hoffman (AMNH).

Diagnosis. Ioscytus chapmani can easily be separated from the other species of *Ioscytus* by the glabrous dorsum and the coloration of the last antennal segment.





The only species that closely resemble *chapmani* are *I. tepidarius* (Hodgden), *I. politus politus* (Uhler) and *I. cobbeni* Polhemus. *Ioscytus tepidarius* differs from *chapmani* in that the texture of the clavus and corium are dissimilar and the clavus is dull, whereas both the corium and clavus of *chapmani* are glabrous. The second antennal segment of both species has long setae and is shaggy in appearance. In both subspecies of *politus* the clavus is sparsely to thickly covered with golden pubescence, and even in submacropterous specimens of *politus flavicosta* Reuter the membrane has more than two closed cells. Specimens of *chapmani* completely lack golden pubescence on the clavus, and have only two closed cells in the membrane. *Ioscytus cobbeni* is probably most closely allied to *chapmani,* but can be easily distinguished by the dull appearance of the clavus and corium; *cobbeni* also differs in that only macropterous forms are known. *Ioscytus chapmani* is allopatric with all congeners, and is the only known species in the eastern United States (Fig. 4).

Etymology. This species is named after Harold Chapman in honor of his contributions to the study of Hemiptera, especially the Saldidae.

Ioscytus tepidarius (Hodgden)

Figs. 1–4

Salda tepidaria Hodgden, 1949:161.
Saldula suttoni Drake and Hussey, 1951:1.
Ioscytus suttoni Polhemus, 1972:143.
Ioscytus tepidarius Polhemus, 1985:139.

Discussion. This species was described on the basis of one specimen from Mexico; the holotype of *tepidarius* in the University of Kansas collection has been studied by one of us (JTP). The type of *suttoni* has also been studied by JTP; this species was synonymized with *tepidarius* by Polhemus (1985). All previous descriptions pertaining to this species by Drake and Hussey (1951), Hodgden (1949) and Polhemus (1972, 1977, 1985) were based on Mexican material known only from the macropterous form. Specimens from northeastern Arizona differ from the Mexican material in that all are smaller and submacropterous; the following description is based on these specimens.

Description. Male: Submacropterous, general color black, oval in shape, dorsum covered with long black erect setae, second antennal segment with long setae, shaggy in appearance.

Head: Black, shining; frons rugulose, orange spot on each side of eye; labrum with orange spot in middle; rostrum dark brown anteriorly, posteriorly half flavous and extending past hind coxae. Vertex and frons covered with numerous black setae of moderate length. Ocelli red, raised and separated by less than the width of an ocellus. Eyes red, almost as wide as long (0.38:0.55). Interocular space equal to the width of an eye (0.37:0.38).

Thorax: Black, shining and smooth; callus raised, with a round depression in middle; sulcus formed by small pits demarcating callus anteriorly and posteriorly;

←

Fig. 3. *Ioscytus chapmani,* habiti: left, adult female; right, immature.

lateral margins slightly reflexed, pile of moderate length setae at anterior edge; posterior lobe rounded. Scutellum as wide as long (0.83:0.83), black, shining and smooth; anterior portion resembles an inverted heart, posteriorly faintly rugose, acuminate distally. Venter black, glabrous; covered with short recumbent golden setae.

Wing: Hemelytra covered with long erect black setae; clavus dull gray except for posterior portion which is black, glabrous; small yellow spot distally on corium near anterior base of second closed cell; embolium leucine to hyaline, extending almost to fracture; black at fracture; membrane dull, black except for outer margins which are leucine to hyaline; with four well developed cells, veins lined with short erect black setae; hind wing well developed, extending past last abdominal segment.

Extremities: Antennal segments dark blackish brown except for yellow distal third of 1st segment; segment 2 longer than remaining three, thickly scattered with long setae, shaggy in appearance; segments 3 and 4 moderately incrassate, thickly set with short dense setae intermixed with scattered long setae. Antennal measurements: I, 0.37; II, 0.80, III, 0.63; IV, 0.67. Legs leucine except for dark brown band on the distal two thirds of femur.

Genital structures: Capsule small, black; parameres small, processus hamatus pointed; corpus paramerus set with long setae; parandria rounded distally. See Figure 1a, b.

Measurements: Mean length of 4♂♂, 4.12, Std. Dev. 0.19. Mean width of 4♂♂, 1.84, Std. Dev. 0.09. Mean length of 4♀♀, 4.62, Std. Dev. 0.09. Mean width of 4♀♀, 2.14, Std. Dev. 0.07.

Female: Similar to male but larger and more robust.

Material examined. (4♂♂, 5♀♀), ARIZONA, Forestdale Trading Post, VII. 3, 1981, C. N. McKinnon (CNM, JTP).

Diagnosis. Ioscytus tepidarius most closely resembles *politus politus* and *chapmani.* It differs from *politus politus* in that it lacks the golden pubescence on the pronotum and clavus and the long erect setae of the second antennal segment. The dissimilar texture of the corium and clavus will separate this species from *chapmani.*

KEY TO THE SPECIES OF *Ioscytus* REUTER

1. Clavus with sparse to thickly scattered golden pubescence 2
– Clavus without golden pubescence 5
2. Inner corium and clavus distinctly dissimilar in texture; inner corium with not more than a few insignificant light markings .... *nasti* Drake and Hottes
– Inner corium and clavus similar in texture; inner corium usually with light markings (some specimens of *franciscanus* without light markings) 3
3. Dorsum not set with long black stiff setae; color black, usually marked with leucine .... *franciscanus* (Drake)
– Dorsum set with long black stiff setae, color black marked with leucine, usually lightly to heavily marked with red 4
4. Posterior lobe of thorax and scutellum moderately to thickly set with golden pubescence; usually submacropterous .... *politus flavicosta* (Reuter)
– Posterior lobe of thorax and scutellum never more than sparsely set with golden pubescence; usually macropterous .... *politus politus* (Uhler)

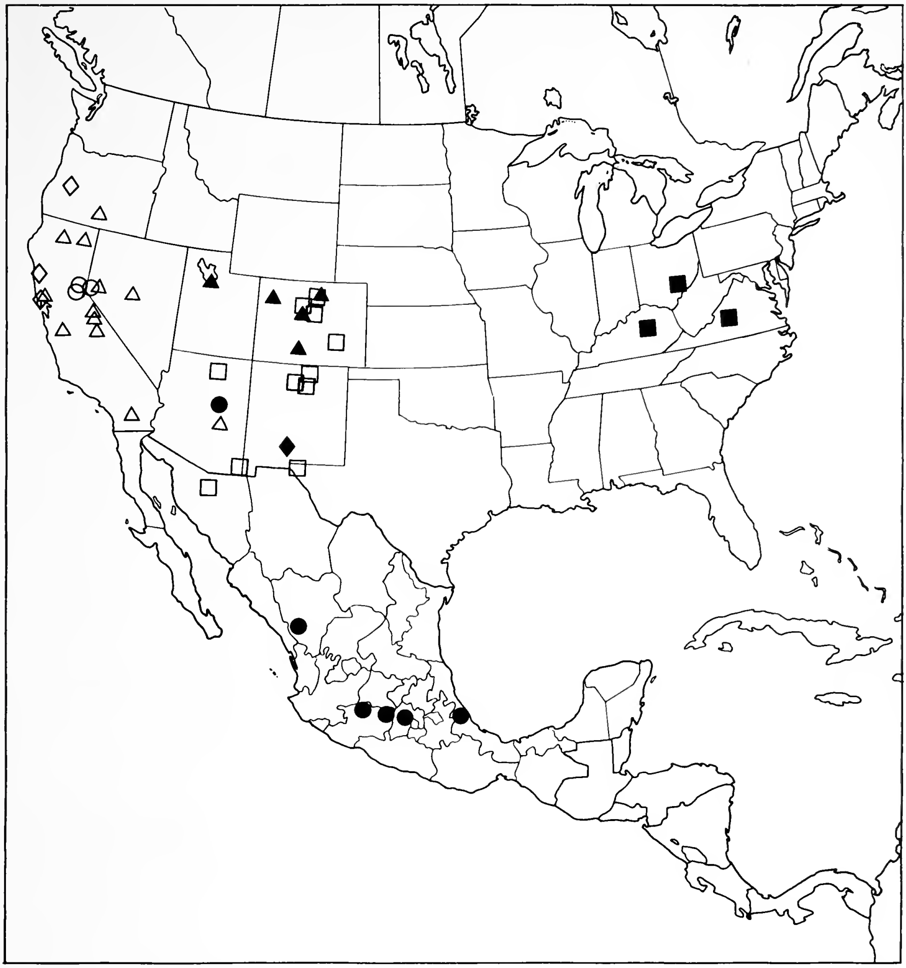


Fig. 4. Distributional map of the genus *Ioscytus*: △ = *politus politus*; ▲ = *politus flavicosta*; □ = *cobbeni*; ○ = *nasti*; ◇ = *franciscanus*; ■ = *chapmani*; ● = *tepidarius*; ◆ = *beameri.*

5. Size less than 3 mm .... *beameri* (Hodgden)
– Size greater than 3 mm 6
6. Dorsum entirely glabrous; fourth antennal segment leucine except for narrow dark basal band .... *chapmani* McKinnon and Polhemus
– Dorsum not entirely glabrous; clavus and inner corium dull to faintly shining; fourth antennal segment black 7
7. Texture of clavus and corium similar, faintly shining, smooth. Antennal segment II not shaggy, without long setae .... *cobbeni* Polhemus
– Texture of clavus and corium dissimilar; clavus dull; corium rugose, faintly shining. Antennal segment II with long setae, shaggy .... *tepidarius* (Hodgden)

HABITAT PREFERENCE

Each species of the genus *Ioscytus* occupies a very specific habitat according to the composition of the substrate and, apparently, prey selection. Most species of *Ioscytus* occupy habitats that seemingly exclude other saldids; thus they are rarely sympatric with other saldid species, even other *Ioscytus* species (except for *cobbeni* and *politus*). This is in marked contrast to other widespread genera such as *Saldula* and *Salda* that commonly have sympatric species. The sympatry of saldid species has been discussed previously by Polhemus (1977, 1985). A brief description of the habitats and some ecological notes are given below by species.

Ioscytus beameri (Hodgden) is at present known only from the type series collected by Dr. R. H. Beamer at Las Cruces, New Mexico. Long ago JTP borrowed his collecting notes which are paraphrased here. The specimens were collected along an irrigation ditch close to the Rio Grande River by pulling up tufts of grass, roots and all, and shaking them vigorously over a white sheet. The bugs were seen only when they ran on the sheet, and were collected in accompaniment with a *Hebrus* species.

Ioscytus chapmani at one locality in Ohio occupies a small grassy seepage area along the banks of a medium-sized lake. This species is positively phototropic in that it was out on sunny days, but took to shelter on cloudy days. The lake was surrounded by an oak-hickory forest within five to ten feet of the bank of the lake. When disturbed, *chapmani* quickly sought the shelter of the forest floor leaf litter. It was only abundant from late August to early September. Earlier collections at the same site in June and July failed to produce any specimens of *chapmani*. In Virginia a single specimen was collected along a marshy area of a small stream in July. This species is only known from the submacropterous form.

Ioscytus cobbeni is distributed from northeastern Colorado to northern Mexico. It prefers small grassy seepages along small streams. In northeastern Colorado this species commonly hides at the base of tall grass blades and is rarely seen in open areas. All specimens collected were macropterous and flew readily when disturbed. This species is prevalent from July to early September.

Ioscytus franciscanus (Drake) is a rare species and our only personal observation is by JTP; in an extensive sphagnum bog near Ft. Bragg, California the bugs occurred only on a small isolated area of wet black earth in the middle of the bog. This bog was surrounded by coniferous forest, all suggesting a highly acidic situation. Data furnished by other workers include wet streamside mud with scattered vegetation, and a marshy meadow, both in Oregon.

Ioscytus politus flavicosta occurs on alkaline substrates along small streams and lakes, and may be found resting on this substrate on bright sunny days. This species is distributed from northeastern Colorado through the northern half of Utah and parts of Nevada. In northern Colorado (Weld Co., Johnstown) this species was for the first time collected with *Ioscytus cobbeni*. After two summers of weekly observations at this site, it became apparent that these two species were occupying different habitats, and the reproductive cycles were not overlapping. *Ioscytus cobbeni* occupied the flat grassy seepage areas of the stream and produced its offspring in July, whereas *politus flavicosta* preferred steep alkaline-encrusted areas on the banks of the stream, and the offspring were dominant in August.

Ioscytus politus politus is common in the far western United States where it usually occurs on alkaline substrates with scattered vegetation and only rarely in other situations. It is sometimes found running over the exposed damp alkaline crust. One specimen was taken from Tomales Bay, California by JTP in close proximity with *Saldula laticollis* (Reuter), *Saldula villosa* (Hodgden) and *Macrovelia hornii* Uhler; this species mix indicates a complex habitat, and in this particular restricted habitat freshwater springs well up in the intertidal marsh.

Ioscytus nasti Drake and Hottes is an uncommon species for which we have only one personal observation (by JTP). It was collected at high elevation (ca. 2,700 m) in a seep area that ranged from dry to wet and was heavily pocked with cattle hoof prints. The vegetation was low and scattered and the water was apparently strictly fresh with no hint of saline or alkaline influence. Dr. Schuh reports *nasti* from streamside damp mud with scattered vegetation at Sage Hen Creek, California.

Ioscytus tepidarius is distributed from Veracruz, Mexico to central Arizona along the Mexican Plateau. The known distribution is very disjunct, as it is based on only a few collections. The specimens from Arizona were collected in early September, but nymphs were observed at this site in early July suggesting that this species overwinters in the egg state. The Arizona habitat is close to the Mogollon Rim and consists of a small spring-fed stream not more than two feet in width that disappears into the ground within one hundred yards of the spring. The specimens were found in the short grassy vegetation along the banks of the stream. No other saldid species were observed at this locality, the type locality of a recently described hebrid (*Hebrus longivillus* Polhemus and McKinnon) and site of the rediscovery of a rare species of chrysomelid.

ACKNOWLEDGMENTS

We wish to thank Richard Hoffman and R. T. Schuh for furnishing the specimen from Virginia and J. D. Lattin for the specimens from Kentucky and the excellent habitus figures of *Ioscytus chapmani* by Bonnie B. Hall which we have used with his permission.

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Received December 28, 1985; accepted March 17, 1986.

J. New York Entomol. Soc. 94(3):442–443, 1986

NOTES AND COMMENTS

PEREGRINUS MAIDIS (HOMOPTERA: DELPHACIDAE) FROM SOUTHERN CHINA

The corn planthopper, *Peregrinus maidis* (Ashmead), has been reported from most of the humid tropical and subtropical regions of the world including the southeastern U.S., the West Indies, Central and South America, Africa, islands in the Indian and Pacific Oceans, India, Malaysia, Taiwan, Indonesia, and Australia (Metcalf, 1943; Anonymous, 1973). This delphacid is a vector of maize stripe virus and maize mosaic virus of corn (*Zea mays* L.) which are economically important to corn production in the tropics and subtropics (Tsai and Zitter, 1982; Falk and Tsai, 1983).

P. maidis was recently collected on corn from southern China, the first record from this region of the world. The collecting data are (m = macropter, b = brachypter, a = apter) PEOPLES REPUBLIC OF CHINA: Guangdong Province, Guangzhou (Canton), 17 October 1984, coll. J. H. Tsai, 4 (m), 1 (b), 1 (a), 2 (m), 3 (b), 5-fifth instars, 5-fourth instars, 2-third instars. One (m) and 1 (b) are deposited in the Department of Plant Protection, South China Agricultural University.

P. maidis males and females typically are dimorphic in regard to wing length with

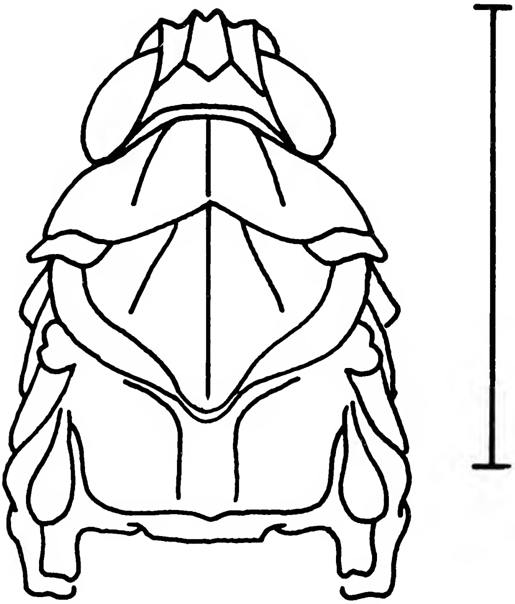

Fig. 1. Dorsal view of head and thorax of apterous male *P. maidis*. Scale = 1.0 mm.

each sex containing macropterous and brachypterous forms (Fullaway, 1918). One male specimen from Guangzhou was entirely wingless (Fig. 1), a condition that has not been reported for *P. maidis*. Completely wingless males and females were found in a population of the sugarcane delphacid (*Perkinsiella saccharida* Kirkaldy) by Osborn (1969).—*James H. Tsai, Stephen W. Wilson and Hwei-Chung Faan, Fort Lauderdale Research and Education Center, University of Florida, IFAS, Ft. Lauderdale, Florida 33314, Department of Biology, Central Missouri State University, Warrensburg, Missouri 64093 and Department of Plant Protection, South China Agricultural University, Guangzhou, Guangdong, China.*

This paper represents Florida Agricultural Experiment Station Journal Series No. 6614.

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J. New York Entomol. Soc. 94(3):443–446, 1986

NEW NORTH AMERICAN RECORDS OF EUROPEAN PARASITOIDS (HYMENOPTERA) OF THE LINDEN APHID, *EUCALLIPTERUS TILIAE* L. (APHIDOIDEA: DREPANOSIPHIDAE)

Lindens (*Tilia* spp.) are frequently planted as shade and street trees, especially in the eastern United States. Although some species in the genus *Tilia* are native to North America, the most common ornamental species in the United States are endemic to Europe (Walheim, 1977). The linden aphid, *Eucallipterus tiliae* L., is also native to Europe, where it feeds only on *Tilia* spp. The first report of *E. tiliae* from North America appeared in 1886 (Olkowski et al., 1982a). This aphid is summer-active and often reaches large population levels in both Europe (Dixon, 1971a, b) and North America (Maino and Howard, 1955; Sunset Books and Sunset Magazines, 1979). Large populations of *E. tiliae* become pestiferous due to the copious amounts of honeydew they produce.

A spectrum of natural enemies are associated with linden aphids in Europe. This note constitutes the first report of two European parasitoids of *E. tiliae* in New York State, one of which has not previously been reported from North America. Mummies from which these parasitoids emerged were collected from little-leaf linden, *Tilia cordata,* on the Cornell University Campus on June 6 and 15, 1985. Specimens of *Trioxys tenuicaudus* Stary were determined using Stary (1978) and the identification was confirmed using specimens determined by the author of this species. *Aphelinus subflavescens* (Westwood) was identified using the generic key provided by Mackauer (1972) and the species description of Ferrière (1965). Voucher specimens of both species have been deposited in the Cornell University Insect Collection under Lot No. 1148.

Trioxys tenuicaudus Stary

Trioxys tenuicaudus belongs to the family Aphidiidae. Stary (1978) reports *T. tenuicaudus* from Czechoslovakia, Latvia, U.S.S.R., and Australia. Introductions of parasitoids of tree-dwelling aphids for biological control were made in northern California in 1972. One shipment included *T. tenuicaudus* which is now established in Berkeley, California and provides control for *Tinocallis platani* on elm trees (Olkowski et al., 1982b).

Trioxys tenuicaudus parasitizes only aphids in the family Drepanosiphidae (*sensu* Heie, 1980). European host aphids and host plants include: *Eucallipterus tiliae* on *Tilia*; *Myzocallis coryli* on *Corylus*; *Tinocallis platani* on *Ulmus*; *Tuberculatus annulatus* on *Quercus robur*; *Tuberculoides* sp. on *Quercus* (Stary, 1978). In Australia, specimens were reared from *Myzocallis castanicola* on *Quercus canariensis* (Carver and Stary, 1974).

Adults of *T. tenuicaudus* are 1.2–2.2 mm long and are distinguished from other *Trioxys* species by the almost hairless dorsal aspect of the prongs which extend from the terminal abdominal sternites (Stary, 1978). Mummies are a golden to bronze color.

Aphelinus subflavescens (Westwood)

Aphelinus subflavescens previously belonged in the monotypic genus *Mesidiopsis* in the family Aphelinidae. *Mesidiopsis* was recently included within *Aphelinus* as a subgenus (Bouček and Graham, 1978). *A subflavescens* is distributed throughout Europe (Ferrière, 1965) and has not previously been reported from North America (Gordh, 1979). I have now identified specimens of *A. subflavescens* from New York State, California, and Oregon. I reared mummies collected in Albany and Berkeley, California from the following host aphids: *Myzocallis coryli* on *Corylus maxima* (VII-30-84, X-1-84); and *Tuberculatus annulatus* on *Quercus robur* (VII-80). Specimens were also reared from mummies of *Myzocallis coryli* on *Corylus* sp. collected on VI-27-84 near Corvallis, Oregon by R. Messing.

Aphelinus subflavescens parasitizes only arboreal aphids. The host range of *A. subflavescens* for both host aphids and tree species they feed on is broader than that of *T. tenuicaudus.* Known aphid hosts in Europe are listed below as well as the genera of host plants most commonly associated with these aphid species: *Hoplocallis pictus, Tuberculoides eggleri,* and *Tuberculatus annulatus* on *Quercus*; *Symydobius* sp., *Kallistaphis* sp., *Betulaspis* [*sic*] (*Betulaphis*?) sp., and *Calaphis* sp. on *Betula*; *Eucallipterus tiliae* on *Tilia*; *Myzocallis carpini* on *Carpinus*; *Drepanosiphum oregonensis* (=*zimmermani*) on *Acer*; *Pterocallis* sp. on *Alnus*; *Myzocallis coryli* on *Corylus* (Patch, 1938; Ferrière, 1965; Richards, 1976).

Adults of *A. subflavescens* are very minute, 0.5–0.9 mm long (Ferrière, 1965). To identify this species, males must be collected. Females are entirely yellow while males have a black marking, usually in the shape of a C, on the distal part of the midtibia. The distal part of the metatarsus of the midleg is also black. Mummies are black and therefore, readily distinguished from *T. tenuicaudus* mummies.

I thank E. R. Hoebeke for reviewing this manuscript.—*Ann E. Hajek, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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Journal of the New York Entomological Society

VOLUME 94 JULY 1986 NO. 3

CONTENTS

Notes and Comments

Vol. 94 OCTOBER 1986 No. 4

Journal

of the

New York Entomological Society

(ISSN 0028-7199)

Devoted to Entomology in General

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The New York Entomological Society
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Meetings of the Society are held on the third Tuesday of each month (except June through September) at 8 p.m. in the American Museum of Natural History, Central Park West at 79th Street, New York, New York.

Mailed October 16, 1986

The Journal of the New York Entomological Society (ISSN 0028-7199) is published quarterly (January, April, July, October) for the Society by Allen Press, Inc., 1041 New Hampshire, Lawrence, Kansas 66044. Second class postage paid at New Brunswick, New Jersey and at additional mailing office.

Known office of publication: American Museum of Natural History, New York, New York 10024.

Journal of the New York Entomological Society, total copies printed 850, paid circulation 700, mail subscription 700, free distribution by mail 18, total distribution 718, 132 copies left over each quarter.

J. New York Entomol. Soc. 94(4):447–457, 1986

HAVE HYMENOPTERAN SOCIETIES EVOLVED TO BE ERGONOMICALLY EFFICIENT?

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Abstract.—Experimental tests of ergonomic theory show that many aspects of ant, bee and wasp societies do not demonstrate maximal ergonomic efficiency. The responses of worker ants to various stresses on their colonies have as often proven not to accord with ergonomic predictions as to support ergonomic ideas. Worker honey bee and stingless bee behavior, and the production of reproductives in vespine wasps, honey bees and ants, provide still less consistent support for ergonomic efficiency arguments. An alternative explanation of hymenopteran social evolution in terms of resiliency can be proposed to explain many of these situations demonstrating constraints upon maximal ergonomic efficiency.

Ergonomic theory proposes that insect societies should evolve to produce the maximum number of reproductive individuals at the least possible cost in sterile worker biomass (Wilson, 1963, 1968; Oster and Wilson, 1978). Wilson and Oster's theoretical framework represents the application of optimal control models from classical macroeconomic theory to the evolution of ants, bees, wasps and termites. Empiricism has lagged behind theory in these regards, but enough data have finally been collected for us to ask: Do social hymenopterans appear to have evolved as ergonomically efficient organisms?

Three aspects of the life history of social insects are recognized in ergonomic theory: colony founding; the ergonomic stage (the production of sterile workers in the optimal proportions of physical or behavioral castes); and the reproductive stage (the production of the maximal number of reproductive individuals, given constraints imposed by either an annual or perennial social organization) (Oster and Wilson, 1978). Data regarding the founding, ergonomic and reproductive stages will be discussed separately for each major group of social insects that have been investigated, to evaluate the applicability of specific ergonomic predictions to various hymenopteran societies.

THE VESPINE WASPS, REPRODUCTIVE STAGE

Ergonomic theory predicts that temperate vespine wasps, as annual colonies, should demonstrate a bang-bang reproductive strategy (Oster and Wilson, 1978). Thus the wasps should invest only in building up a force of workers until the final generation of the season, and then use that worker force to produce nothing but reproductives.

Greene (1984) described the production schedules of six species of temperate zone vespine wasps (*Vespa orientalis, V. crabro, Dolichovespula maculata, D. arenaria, Vespula atropilosa, V. vulgaris*) and found that the wasps begin to produce reproductives before the midpoint of their colony life cycle. They produce workers and reproductives side-by-side for a considerable period of time. He points out that this may "limit the risk of total loss" which could occur if a colony was disrupted before any reproductives could be produced (Greene, 1984).

Greene (1984) also demonstrated that Macevicz and Oster (1976) inadvertently mistranscribed data originally presented by Ishay et al. (1967), and that therefore the data from *Vespa orientalis* that the former authors presented as support for the bang-bang model of reproductive output were erroneous. *V. orientalis* reproductive production overlaps with worker production, and so it is not an ergonomically efficient species (Ishay et al., 1967; Greene, 1984).

THE HONEY BEES, REPRODUCTIVE STAGE

Perennial social insect colonies are predicted by ergonomic theory to have repetitive yearly cycles with exclusive worker production at first, followed by a later period of exclusive reproductive production. This is merely a bang-bang model repeating itself for every year of a colony's life (Oster and Wilson, 1978). As in an annual colony, this should allow a large worker force to be built up and then utilized for queen and drone production.

Honey bees have perennial colonies (Seeley, 1978). Thus, to support ergonomic theory, they should fall into Oster and Wilson's (1978) pattern of repetitive bang-bang cycles of reproductive production.

Temperate honey bees produce their new queens early in the summer months (Michener, 1974) rather than at the end of the warm season as ergonomic theory would predict. It is almost certainly crucial for new honey bee colonies to get started early in the growing season, so that they can sequester sufficient food reserves to survive the next winter. Production of the maximal number of reproductives via a repetitive bang-bang strategy does not appear to be more important than providing new colonies with adequate time to prepare for the challenge of winter. Overwintering survival supplies an important constraint upon maximal efficiency in reproductive production.

THE HONEY BEES AND STINGLESS BEES, ERGONOMIC STAGE

Ergonomic theory makes several predictions about maximally efficient division of labor among worker bees. These include (Oster and Wilson, 1978):

1) Although only one physical caste of workers is present in most bee species, there should nonetheless be specialization among the workers to increase their efficiency. This argument is based upon the increased reliability afforded by specialization resulting in simpler tasks for each individual worker.

2) The minimum sterile worker biomass needed to run the colony should be produced, as any extra workers in "a large standby reserve" would require "a more bountiful environment to support what can be characterized as ergonomic inefficiency" (Oster and Wilson, 1978).

3) Workers should divide tasks within a colony in accord with spatial segregation of materials (brood cells, pollen cells, honey cells, etc.). This lessens the energy expended by workers moving between distant task sites.

4) In order to be most efficient, social organization of the workers should be "teamless," i.e., workers performing the same task(s) should be interchangeable with one another.

5) Foraging workers should maximize the amount of material gathered while minimizing the energetic cost of collection.

For the sake of clarity, the data regarding each testable prediction of ergonomic theory will be discussed in numerical order.

1) Lacking physical castes, there are two ways that worker bees could be specialized. (a) They could be individual specialists with one bee performing a certain task more than any other tasks, or (b) they could possess an age-related sequence of duties (age polyethism) so that each worker passes through the same sequence of tasks as it matures.

(a) Only a few percent of the workers performing hive duties in a honey bee colony are individual specialists. Visscher (1983) reported that "undertaker bees" who remove corpses of dead hive mates account for one to two percent of a colony. Winston and Punnett (1982) reported that a few hive workers groomed other workers as their primary task. Kolmes (1985a) performed an information-theory analysis of individual task specializations among hive bees, and found a low divergence from independence (D_2) indicating that there are no detectable individual specializations among the majority of hive workers.

When workers become older they leave the hive and undertake foraging duties. Individual specialization among foragers has been well documented (Seeley, 1983; Ribbands, 1952; Sekiguchi and Sakagami, 1966; Lindauer, 1952) as discussed in Kolmes (1985a). Several explanations have been proposed for why individual specialists exist among foragers but not among younger hive bees (Kolmes, 1985a).

(b) The age-related transition among honey bees from hive bee to forager has been well documented (Rösch, 1925, 1927, 1930; Sakagami, 1953a, b; Sekiguchi and Sakagami, 1966; Winston and Punnett, 1982). Seeley (1982) found that young hive bees were nonrandomly distributed in the hive, but did not demonstrate statistically significant behavioral transitions among hive workers. Kolmes (1985b) using whole-repertoire statistics, demonstrated a significant behavioral transition between hive bees and foragers, but no behavioral sequence earlier during the hive period. Again, possible explanations for the lack of age-related specialization among hive bees are given in Kolmes (1985a).

2) Hive bees in experimentally wax-deprived honey bee colonies were able to perform significantly more of several behavior patterns involved in replacing the missing cells, while not performing significantly less of 25 other behavior patterns compared to control colonies (Kolmes, 1985c). This is evidence for a reserve of uncommitted efforts and therefore for a situation characterized by "ergonomic inefficiency" (Oster and Wilson, 1978). Reserve forces are also suggested by changes in temporal caste structure following incidents of worker loss (Winston and Fergusson, 1984).

3) Sommeijer (1982 and in press) reported that workers of the stingless bee *Melipona favosa* constructing brood cells repeatedly travel over much of the hive to interact with the queen. This is not in accord with a minimization of energy expended in "commuting" in this eusocial insect. The need for social integration is a constraint upon energetic efficiency here, and so energetic expenditures in communication between the queen and cell builders are maintained.

Seeley (1982) found a nonrandom spatial distribution of differently aged worker honey bees within the hive. Although this indicated some order in the system, it differed from a maximally efficient system. Worker bees of every age were present for considerable proportions of their time in widely separated parts of the hive, rather than minimizing "commuting" expenditures.

4) Foraging groups among worker honey bees performing field duties (Frisch, 1967) are composed of "teams" of noninterchangeable individuals. These foraging group "teams" are contrary to ergonomic predictions. In the stingless bee *Melipona favosa* "teams" of workers that build larval cells are subsequently responsible for provisioning them (Sommeijer et al., 1982). These "teams" also exist contrary to ergonomic theory's expectations.

5) Maximally efficient foragers should collect nectar loads with the greatest energetic return per unit energetic expenditure in foraging. Schmid-Hempel et al. (1985) found that worker honey bees maximize their energetic efficiency (although not their rate of food gathering) by only partially filling their crops before returning to the hive. Seeley (in press) has also provided evidence that honey bee foragers maximize net energy gain rather than net energy intake rate. These independent and consistent studies demonstrate what appears to be an ergonomically efficient foraging technique.

THE ANTS, REPRODUCTIVE STAGE

Leptothorax longispinosus is a facultatively polygynous ant. Colonies with multiple queens could be ergonomically more efficient due to either of the following: (1) Increased genetic and therefore phenotypic worker variability might enhance the potential for morphologically based task specialization among the workers, or (2) multiple queens might increase the overall level of reproductives produced. In fact, Herbers (1982) found that neither of these conditions are met. Multiple-queen colonies have no greater phenotypic variability among workers, and these colonies actually have a lower production of reproductives than single-queen colonies. Multiple queens in *L. longispinosus* exist therefore in contradiction to ergonomic predictions.

Amblyopone pallipes is a primitive ant with small colonies of carnivorous habit. *A. pallipes* rears only one brood of ants per year, containing both workers and reproductives (Traniello, 1978). This is contrary to a bang-bang model of initial worker production followed by reproductive production.

Some ants have annual swarming cycles that may be in accord with ergonomic predictions of a bang-bang production of reproductives (*Myrmecia* spp., *Myrmica rubra*) while other ants produce reproductives year-round (*Monomorium pharaonis*) (Wilson, 1971). Much more needs to be known about events within ant colonies over an annual cycle before any more generalizations can be made.

THE ANTS, ERGONOMIC STAGE

This largest part of the empirical literature that pertains to ergonomic theory can be divided into several segments. Firstly, many papers exist that demonstrate systems of caste diversity potentially consistent with ergonomic predictions (Table 1). These papers describe worker castes that are *necessary but not sufficient* to support ergonomic predictions. This literature points out many potential systems for future use in critical evaluations of ergonomic theory.

Table 1. Papers reporting morphological and/or temporal worker castes in ants. These should be viewed as evidence of polyethism, rather than as critical support for ergonomic predictions.

Brandao, C. D. (1978)	*Formica perpilosa*
Busher, C. E., P. Calabi and J. F. A. Traniello (1985)	*Camponotus sericeiventris*
Calabi, P., J. F. A. Traniello and M. H. Werner (1983)	*Pheidole hortensis*
Carlin, N. F. (1981)	*Orectognathus versicolor*
Corn, M. L. (1980)	*Cephalotes atratus*
Gordon, D. M. (in press a)	*Pogonomyrmex badius*
Herbers, J. M. and M. Cunningham (1983)	*Leptothorax longispinosus*
Mirenda, J. T. and S. B. Vinson (1981)	*Solenopsis invicta*
Topoff, H. (1971)	*Eciton, Neivamyrmex, Aenictus*
Wilson, E. O. (1976)	*Pheidole dentata*
Wilson, E. O. (1978)	*Solenopsis invicta*
Wilson, E. O. (1980a)	*Atta sexdens*

Secondly, some studies have provided data inconsistent with ergonomic predictions (Traniello, 1978; Wilson, 1983a, 1984, 1985b; Rissing and Pollock, 1984). Thirdly, some studies have provided data supporting ergonomic predictions (Herbers, 1980; Porter and Tschinkel, 1985; Wilson, 1980b, 1984, 1985a; Davidson, 1978; Gordon, in press b). These two groups of papers will be briefly mentioned one at a time.

Amblyopone pallipes is a primitive ant species; its colonies consist of a queen and from 9 to 16 workers (Traniello, 1978). The workers appear to behave in a fashion counter to ergonomic predictions in two ways: (1) Workers perform tasks both within and outside the nest simultaneously, rather than working within spatially circumscribed regions; (2) age polyethism is nonexistent, workers contribute evenly to performances of every task in the colony. The lack of a complex division of labor in *A. pallipes* may be correlated to its small colonies and reliance on centipedes and beetle larvae for prey. Some ants must go out to hunt, which may not leave the worker resources that would be required to establish a separate brood-tending caste.

Atta cephalotes is a leaf-cutter ant; ergonomic theory predicts that if some of the energetically most efficient leaf-cutters (media workers with head widths 1.8–2.2 mm) are removed from a colony, then the colony should respond by having a greater proportion of workers from adjacent head size classes (head widths of 1.6 mm or less, and of 2.4 mm or more) join the foraging force (Wilson, 1983a). Rather than fulfilling this prediction, ants already present in the foraging force merely began to work harder. Foragers with head widths above or below the optimum for leaf cutting acquired more access to leaf edges, and the surviving optimum-sized workers (1.8–2.2 mm head widths) increased their foraging activity by roughly five times (Wilson, 1983a). The foraging force was therefore ergonomically highly inefficient prior to the experimental manipulation.

Having discussed the ergonomic inefficiency revealed in *Atta cephalotes* foragers by experimental manipulations, it is surprising that in *A. sexdens* the foraging groups are largely made up of workers with head sizes making them the most energetically efficient leaf-cutters in the colony (Wilson, 1980b). When workers of *A. sexdens* were examined while cutting leaves of a tough consistency (rhododendron) the size class of workers that were: (a) Most energetically efficient leaf-cutters in terms of construction costs of workers and, (b) most energetically efficient leaf-cutters in terms of maintenance costs of workers, proved to make up the great majority of the foraging groups (Wilson, 1980b). We can only speculate as to whether or not *A. sexdens* foragers would continue to conform to ergonomic predictions if they were tested by removal experiments like those performed on *A. cephalotes* (Wilson, 1983a).

Formica obscuripes, a mound-building formicine ant, responded to two types of long-term experimental stress (artificial predation and resource depletion) with shifts in the frequencies of its media and major workers (Herbers, 1980). This is consistent with the ergonomic prediction that in an insect society possessing morphological castes, long-term stresses should be responded to by shifts in caste ratios.

Pogonomyrmex barbatus, the red harvester ant, responded to interference or removal experiments involving one worker group (nest maintenance, foragers, etc.) with changes in temporal patterning of behavior and in levels of various activities. Priority patterns exist among behavioral responses to environmental stresses (Gordon, in press b). This responsive redistribution of effort is consistent with ergonomic predictions.

Solenopsis invicta, the fire ant, has a natural worker caste polymorphism that results in efficient brood production (Porter and Tschinkel, 1985). Laboratory colonies containing a caste mixture typical of *S. invicta,* and monomorphic small-worker colonies, produced more brood than monomorphic medium-worker or large-worker colonies. The polymorphic colonies were approximately 10% more efficient at brood production in energetic terms than were the monomorphic small-worker colonies. These data support predictions of ergonomic efficiency in ant colony caste structure. Interestingly a fairly high percentage of the variance in experimental results was also related to colony identity; ant colonies appear to be idiosyncratic in some aspects of brood rearing.

Various aspects of social organization in the genus *Pheidole* appear to conform to ergonomic predictions, while other empirical results are distinctly not ergonomic. Major workers of *P. megacephala, P. guilelmimuelleri* and *P. pubiventris* expand their behavioral repertoire and increase their activity levels if minor workers are removed (Wilson, 1984). In *P. pubiventris* the mechanism mediating this shift appears to be an active avoidance of minor workers by major workers in the vicinity of the brood pile (Wilson, 1985a). These behavioral shifts conform to ergonomic predictions.

Minor workers of *Pheidole guilelmimuelleri* and *P. pubiventris* do not alter their repertoire or activity levels if the proportion of major workers present in their colony is manipulated (Wilson, 1984). This insensitivity does not conform to ergonomic predictions.

Ergonomic predictions about worker caste behavioral repertoire breadth in terms of body size provided equivocal results in *Pheidole* (Wilson, 1984). This topic cannot be discussed definitively until more data have been collected.

Major workers of *Pheidole dentata* are specialized for defense against *Solenopsis* (fire ants and congenerics). When *P. dentata* colonies are challenged continually with a *Solenopsis* threat, contrary to ergonomic predictions the major-minor worker ratio remains unaltered (Johnston and Wilson, 1985; Wilson, 1985b).

Veromessor pergandei presents us with a case of ambiguous results. For colonies present at three out of four field sites Davidson (1978) found that worker mandible lengths were significantly positively associated to the sizes of seeds being transported. The distribution of worker sizes was also responsive to the interspecific competitors which were present (Davidson, 1978). Rissing and Pollock (1984) could find no evidence of a correlation between seed size and worker size at one field site. This may be an instance where whether or not ergonomically efficient behavior is displayed depends upon environmental factors.

THE ANTS, FOUNDING STAGE

Atta cephalotes colonies progress in their early ontogeny from a size distribution of workers that parsimoniously allows both vegetation collection and fungus harvesting, to a broader range of worker sizes in older colonies (Wilson, 1983b). This is in accord with the type of adaptive demography predicted by ergonomic theory (Oster and Wilson, 1978) although more definitive data produced by experimental manipulations and measurements of colony growth rates remain to be collected (Wilson, 1983b).

CONCLUSIONS

The evidence collected to date supports ergonomic theory in the responses of worker ants to certain experimental stresses (Wilson, 1980b, 1984, 1985a; Porter and Tschinkel, 1985; Davidson, 1978; Herbers, 1980; Gordon, in press b) but not in other situations (Wilson, 1983a, 1984, 1985b; Rissing and Pollock, 1984; Traniello, 1978). Ergonomic efficiency is an apt description for only specific aspects of worker ant evolution; it is apparent that rather than generalizing it will be necessary to proceed case-by-case in applying ergonomic ideas to worker ant behavior.

Worker honey bees and stingless bees have generally provided evidence contrary to ergonomic efficiency arguments (Sommeijer et al., 1982; Frisch, 1967; Sommeijer, 1982 and in press; Kolmes, 1985a, b, c). Ergonomic theory has proven to be applicable so far in one situation when worker bees were considered, in the partial filling of their crops by honey bee foragers (Schmid-Hempel et al., 1985) and in maximizing net energy gain (Seeley, in press; Schmid-Hempel et al., 1985).

Production schedules for reproductives in some ants may correspond to the ergonomic bang-bang efficiency model (Wilson, 1971) but there is evidence contrary to ergonomic predictions for other ant species (Herbers, 1982; Traniello, 1978). Both temperate vespine wasps (Greene, 1984) and bees (Michener, 1974) fail to correspond to ergonomic predictions in their production of reproductives.

In many of the situations that are not ergonomic, it is apparently a need to counter environmental challenges in a resilient manner that has prevented ergonomically efficient hymenopteran societies from evolving. Temperate vespine wasps and honey bees produce queens earlier than ergonomic theory would predict. For the wasps this prevents a total loss of reproductive output should a colony fail during the summer and for honey bees this allows enough time for newly swarmed colonies to sequester adequate food reserves to survive the following winter (Greene, 1984; Michener, 1974). The long distances traversed by stingless bee workers in the hive (Sommeijer, 1982 and in press) and the existence of foraging groups of worker honey bees (Frisch,

1967) probably represent a trade-off of increased social integration for somewhat decreased worker efficiency. These processes allow stingless bee workers to monitor the queen's condition as they construct cells, and honey bee workers to be rapidly recruited by foragers visiting the same floral resource (Sommeijer, 1982 and in press; Frisch, 1967). *Atta cephalotes* foragers and honey bee workers both behave in a fashion contrary to maximal energetic efficiency in maintaining large reserve forces that are only brought into play following presentation of some sort of stress to the colony (Wilson, 1983a; Kolmes, 1985a). Both of these situations reflect hymenopteran societies with considerable resiliency, which can meet and overcome environmental challenges but which are ergonomically inefficient otherwise.

The latter examples are reminiscent of Slobodkin's (1964) description of evolution as an "existential game." Any organism that perpetually overcomes environmental challenges and reproduces itself will be the ultimate "winner" simply by failing to go extinct. If one volleyball team always gets the ball over the net the opposing team will lose, because eventually they will fail to return the ball. When the opponent in the game is the changing environmental parameters and competitors presented by a passage through geological time it is doubtful if any species can survive indefinitely, but examples of resiliency rather than ergonomic efficiency may well represent evolutionary adaptations for "staying in the game" rather than trying to "spike the evolutionary ball."

Resilient social structures trade energetically optimized caste systems for the ability to respond to environmental challenges and perturbations. If large investments in mechanisms promoting resiliency have placed constraints upon the evolution of maximal ergonomic efficiency in insect societies, where might we expect this resilient type of social organization to be most visible? There are several situations in which, *a priori,* we would predict resilient systems to have evolved: (1) Resiliency would be expected to evolve where biotic components of the environment pose potentially catastrophic threats, such as the army ant columns that appear to have resulted in the energetically expensive multiple nest construction of *Pheidole desertorum* (Droual, 1984). (2) We might expect a greater investment in resiliency for colony defense in species that occupy exposed nesting sites as opposed to protected nesting sites. Seeley et al. (1982) described such nesting habits for *Apis dorsata* and *A. cerana* respectively. Jeanne (1975) and Michener (1964) described other wasp and bee nesting habits that could be predicted to rely more or less upon behavioral defenses that would require resilient social structures. (3) Swarm founding species among the bees, ants, and wasps produce individual reproductive units that are very costly compared to the reproductive units of species with solitary colony founding. Defense of the valuable and relatively exposed swarms should promote the evolution of considerable resiliency in swarm organization. See Lee and Winston (1985a, b) for an indication of how valuable large swarms are in one bee species. (4) Perennial colonies in seasonal climates are presented with a greater range of climatic challenges than are annual species or perennial species in tropical environments (Winston et al., 1983), and the former can be predicted to have evolved resiliency-enhancing mechanisms to meet the demands of these challenges. (5) Species which exploit transiently abundant resources should have social systems with reserve forces available for rapid resource exploitation, and in addition may be expected to have evolved energetically costly mechanisms of intracolony communication to provide integration for rapid resource exploitation. See Visscher and Seeley (1982) for one discussion of foraging strategies in shifting food patches. In all of the preceding situations, resilient social systems can be predicted to have evolved, thus placing constraints upon the evolution of maximal ergonomic efficiency in insect societies. More empirical comparisons will be needed before we understand the mixtures of resiliency and energetic optimization that various selective pressures have produced in insect societies.

ACKNOWLEDGMENTS

I am thankful to three anonymous reviewers for their useful and careful comments about an earlier version of this paper.

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Received October 25, 1985; accepted March 21, 1986.

J. New York Entomol. Soc. 94(4):458–466, 1986

THE BIOLOGY OF A SUBTROPICAL POPULATION OF *HALICTUS LIGATUS* IV: A CUCKOO-LIKE CASTE

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Abstract.—Intraspecific cleptoparasitism is described in a subtropical population of the social sweat bee *Halictus ligatus*. Cuckoo-like individuals are, on average, larger than workers but smaller than queens. Behavioral modifications resulting in the cleptoparasitic behavior are quite minor: forced entry and sneaky oviposition are activities possessed by non-parasitic members of this population. Only the trap-lining and host nest choice behaviors are new. Intraspecific cleptoparasitism has not been recorded from any of the temperate populations of this species that have been studied. It is argued that the continuously brooded, multivoltine phenology of this population has been a necessary prerequisite for the origin of this pattern of cleptoparasitism.

A large number of bees exhibit obligatory cleptoparasitic behavior, that is they do not provision their own nests but lay eggs in those built and provisioned by other species (Bohart, 1970). The success of this strategy is indicated by the fact that whole genera and even tribes of bees are obligate cuckoos (Michener, 1944; Bohart, 1970). Most cleptoparasites lay their eggs in the nests of solitary hosts. However, cleptoparasitism of social hosts is a fairly common condition, exhibited particularly frequently by parasitic species of the subfamily Halictinae whose hosts are usually other species of this taxon (Michener, 1977). Over half of the records assembled by Michener involve hosts that are known to exhibit eusocial behavior. However, most halictines that have been studied in any detail are social species, therefore the sample is biased in favor of cleptoparasites of social hosts. True social parasitism, in which the intruding parasite becomes an integral part of the host society, is a rarer phenomenon in bees: known in the cuckoo bumble bees of the genus *Psithyrus,* various allodapines (Wilson, 1971) and in *Microsphecodes* (Eickwort and Eickwort, 1972) and some *Sphecodes* (Knerer, 1980).

Although there are several reports of intraspecific nest usurpation within the Halictinae (Knerer, 1973) and elsewhere amongst the social Hymenoptera (Archer, 1980; Fisher, 1985; Richards, 1978; Turilazzi, 1985) intraspecific cleptoparasitism has not been recorded for any social species, but is known in solitary forms (Eickwort, 1975). Emery's rule: "that parasitic species tend to resemble their host species more than any other free-living form" (Wilson, 1971) seems to hold true for most cleptoparasitic halictine taxa. Apparent exceptions, such as the large and cosmopolitan genus *Sphecodes,* result from a long evolutionary history of cleptoparasitism: the ancestral *Sphecodes* almost certainly parasitized a host that was a closely related halictine species. Thus, intraspecific cleptoparasitic behavior should provide important clues as to the origin and further elaboration of this mode of life.

Detailed field investigations were carried out on the bionomics and social organization of *H. ligatus* at Knights Key, Monroe County, Florida between February

1981 and February 1984 (see Packer and Knerer, 1986a for an account of the general biology of this population). This paper is an account of cuckoo-like behavior in a small proportion of the individuals in this subtropical population.

METHODS

On the 22nd of December 1981 a large individual of *H. ligatus* was observed to circle around the entrance of a conspecific nest. Several times on that day this bee flew to the nest from the north east, flew around the entrance several times and then circled around another nest two meters away. This trap-lining behavior is characteristic of cleptoparasitic species and was observed as closely as possible thereafter.

Trap-lining behavior was distinct from other types of searching behavior exhibited by young gynes looking for a suitable nest site or lost foragers attempting to find their nest. Searching young gynes carefully inspected certain areas, first whilst on the wing and then by walking. They then moved on a short distance (rarely more than 30 cm unless suitable substrate was absent) and repeated the process. Eleven such searching young foundresses were captured, although more were seen (Packer and Knerer, 1986a). Lost foragers would repeatedly search the same area in flight, alight frequently but fly off every now and then only to return after re-orientation. This type of searching behavior was observed on many occasions in the course of this study but always after a bee had been disoriented by capture or after its nest entrance had been obstructed.

The behavior of trap-lining individuals was very different from either of these searching activities. Trap-liners flew low over the ground, from nest entrance to nest entrance, without any hesitation. The paths that they took appeared stereotyped, as if they "knew" where the nest entrances were, and were repeated several times daily, and on at least two occasions, over several successive days. Additionally, most of the observations of trap-lining took place before any nest excavations had been performed and in a comparatively undisturbed part of the study site: these were not lost bees.

During the course of the rest of the study, some 24 trap-lining individuals were caught and preserved in Kahle's solution. Their head widths, wing and mandibular wear and reproductive condition were noted as described by Packer and Knerer (1986a). Ovarian status was assessed following Litte (1977) and Michener and Bennett (1977). Thus, females were divided into categories with five or six (A), three or four (B), one or two (C) or no (D) developed ovarioles. Furthermore, each ovariole was assessed as to whether its contents were developing or being resorbed, these conditions being distinguished by shape and coloration (Packer and Knerer, 1986a). These data were used to compare trap-lining bees with queens and workers from excavated nests.

RESULTS

Trap-lining females were significantly smaller in size than queens (t test with Sidak's multiplicative inequality [Rohlf and Sokal, 1981], $t = 2.45$, $P < 0.05$), and significantly larger than workers (same test as above, $t = 7.63$, $P < 0.01$) excavated from nests (mean head width of queens = 3.63 mm, SD = 0.19, N = 50; trap-lining bees 3.49 mm, SD = 0.25, N = 24; workers = 3.09 mm, SD = 0.20, N = 322). The size variation of these three categories of female can be seen in Figure 1.

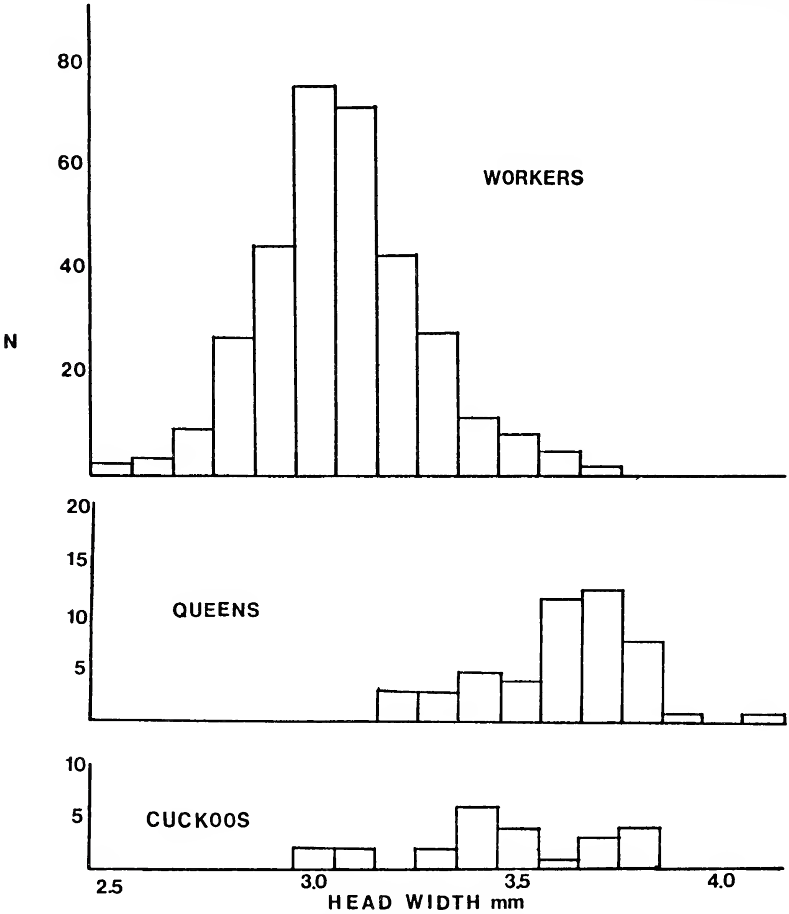

Fig. 1. Size variation in queens, workers and cleptoparasitic females of *H. ligatus* at Knights Key, Florida.

Only 2 of the 24 trap-lining individuals had any mandibular wear, significantly fewer than queens or workers (Fisher's exact test, $P = 0.0009$ and $P = 0.015$ respectively). In contrast, 13 of the 24 trap-liners had some wing wear, varying from one or two nicks in the wing margin to having the complete margin frayed away. There was no significant difference in the degree of wing wear between these individuals and queens and workers from nests.

Like queens, all of the trap-lining females were mated (in this population 58% of the workers were mated). Trap-lining bees differed in the number of developed ovarioles when compared to workers but not when compared to queens (Table 1). No queens or trap-lining bees had fewer than two developed ovarioles and the relative frequency of occurrence of ovarian categories A, B and C did not differ significantly between the two groups ($\chi^2 = 3.09$, $P > 0.1$). Worker individuals showed a much higher proportion of ovarian categories C and D than trap-lining bees ($\chi^2 = 20.05$,

Table 1. Variation in the frequency of ovarian categories in queens, workers and cuckoos of *H. ligatus* at Knights Key. Figures in brackets are percentages. With ovarian categories A and B, and C and D combined, differences between queens and cuckoos are not significant (Fisher's exact test, $P = 0.34$), those between workers and cuckoos are highly significant ($\chi^2 = 18.5$, $P < 0.0001$).

	Ovarian category			
	A	B	C	D
Workers	22 (8.3)	78 (29.4)	85 (32.1)	80 (30.2)
Queens	25 (62.5)	11 (27.5)	4 (10.0)	0 (0.0)
Cuckoos	8 (33.3)	12 (50.0)	4 (16.7)	0 (0.0)

$P < 0.0001$). Queens and workers did not differ significantly in the relative proportions of ovarioles with developing or resorbing contents (with 42.4 and 39.5% of enlarged ovarioles containing developing contents respectively). However, trap-lining bees had mostly developing oocytes (67.7% of enlarged ovarioles), differing significantly from workers and queens combined ($\chi^2 = 14.81$, $P < 0.0001$).

The following sequence of events was observed around the entrance of one nest which was situated in an unusually open position: in an area of very short and sparse grass cover. This nest was comparatively populous: nine foragers had been marked and the duration of their pollen foraging trips was being recorded when these observations were made. Another two, small, unmarked bees were also foraging from this nest. On the 23rd of December 1981 the same large bee that was first observed trap-lining on the 22nd regularly visited the same nest between 1115 and 1320 hrs. It was first observed at 1115, and then at 1149, 1225 and lastly at 1310 hrs. During each visit, it entered the nest entrance briefly before leaving. On the 29th of December a large bee (quite probably the same individual, judging by relative size and details of flight behavior) entered the nest, flying from a height of 30 cm straight down into the entrance at 1232 hrs. Only one forager left the nest after this and the nest was plugged at 1329 hrs (it is not known which bee was responsible for the nest closure). On two other occasions the nest was observed to be still open at 1500 and 1530 hrs. At 0900 hrs the following morning a large bee was gradually forced out of the nest; it was captured and preserved. Upon dissection this individual appeared to have oviposited recently: one ovariole remained oocyte-shaped but was empty. It seems likely that it was the intruder observed the day before.

On the 5th of January at 1210 pm the same type of rapid entrance was again exhibited by a trap-lining individual. Three bees that had been observed foraging earlier in the day were evicted and the nest entrance was plugged soon afterwards. An additional three returning pollen-laden foragers joined the evicted bees in trying to locate the nest entrance, succeeding approximately 15 minutes later. At this point I attempted to excavate the nest but unfortunately the burrow went down a narrow fissure in the coralline substrate and complete excavation was impossible. Other interactions between trap-lining bees and individuals at nests were restricted to brief encounters at nest entrances before the former were captured.

Nests of *H. ligatus* at this locality are frequently guarded although no individuals seemed to be specialized in this task. Most guarding bees stayed at the nest entrance for only short periods of time, often returning deeper into the nest or leaving to forage. Individuals spend longer periods of time guarding as a result of disturbances at the nest entrance—caused by ants, cuckoo bees or returning young gnyes; such individuals would rarely be observed guarding with such intensity for more than a few hours. Guarding seems to be facultative in this population.

DISCUSSION

Trap-lining *H. ligatus* females at Knights Key have a relatively high degree of ovarian development with very little ovarian resorption compared to queens and workers in nests. They exhibit hardly any mandibular wear, a wide range of wing wear and all of them are mated. Observations at one particular nest entrance indicate that these bees forcibly enter populous nests. It seems probable that these individuals represent a cleptoparasitic subpopulation of this species. They are clearly not searching young foundresses, as indicated by the difference in searching behavior and the high degree of ovarian development and, in many individuals, large amount of wing wear in the trap-lining bees. It is noteworthy that the trap-lining bees had as much ovarian development as queens in nests with active foragers, more than gynes that were provisioning their first brood. Trap-lining bees were not foraging workers as they did not carry pollen loads, were in general much larger and seemed to have a clear route between nests that they would follow over several days. Neither were they lost bees, the behavior patterns of which are very different.

Intraspecific nest usurpation is a well known phenomenon in social Hymenoptera (Archer, 1980; Fisher, 1985; Plowright and Laverty, 1984; Turilazzi, 1985) and has been recorded from social halictines (Knerer, 1973). The behavior reported here for *H. ligatus* is thought to represent cleptoparasitism and not nest usurpation for several reasons. Firstly, halictine females do not undergo ovarian development until they have a nest suitable for provisioning. This is shown by the results of dissections of searching young foundresses from the same locality (Packer and Knerer, 1986a). It is unlikely that a usurping individual of *H. ligatus* will develop oocytes until after a nest is usurped. All of the trap-lining females that were dissected had at least two ovarioles with well developed contents. Furthermore, usurpers may be expected to oust an original owner before reaching a comparatively old age. The fact that several of the trap-lining bees had very worn wings indicates that if they were usurpers, they must be comparatively unsuccessful ones. In addition, the only forced nest entrances observed took place in populous nests, this would not be the strategy that one might expect a usurper to adopt. For these reasons it is thought that the observations recorded here represent cleptoparasitic behavior. Nonetheless, the possibility that usurpation occurs at this locality cannot be disproven; however, it was not observed.

It has been shown that the amount of mandibular wear correlates well with the amount of excavation performed by individual females of this species (Packer and Knerer, 1986b). The low degree of mandibular wear in cuckoo-like individuals of *H. ligatus* at Knights Key indicates that they perform little or no excavation. The large proportion of searching cuckoos with a high degree of wing wear indicates that they probably do not stay in one nest for any great length of time, unlike *Psithyrus* species (Fisher, 1984) or some species of *Sphecodes* (Knerer, 1980). Rather, it seems more likely that they oviposit in several nests over a protracted period of time, as appears to be the case with *Microsphecodes kathleenae* (Eickwort and Eickwort, 1972).

Trap-lining *H. ligatus* females are comparatively large and therefore, the egg that produced them must have been laid upon a large pollen mass. Large provision masses are characteristic of the queen production phase of colony development. In this population, gyne production occurs when the nest population is near its maximum (Packer and Knerer, 1986a). Therefore, if the tendency towards cleptoparasitism is heritable, such individuals must attempt to enter the more populous nests. Alternatively, if this behavior is facultative, forced entry into the more easily invaded smaller nests may be expected. In such instances, the cleptoparasite could lay male-producing haploid eggs on the smaller male or later worker-producing pollen balls. In addition, the oviposition of diploid eggs on smaller provision masses may not be particularly disadvantageous because of the high degree of worker oviposition at this locality. In either case, trap-lining is the mechanism allowing repeated assessment of potential host colonies. Large colonies were the targets of both of the invasion attempts that were observed. Although obtaining entry into populous colonies may be more difficult, the complexity of the nest burrows and general social chaos that may characterize these nests probably makes it more likely that oviposition by a cuckoo will pass undetected than in a younger, less populous nest.

Of particular interest is the low degree of ovarian resorption in the cuckoo individuals. Two reasons may be suggested for this. Firstly, it may be expected that cleptoparasitic individuals are selected to be able to retain developed oocytes for a comparatively long time before they begin resorption. This would allow them more time to find a suitable nest to parasitize. Secondly, the high degree of ovarian resorption in queens and workers in nests may result from mutual inhibition (and there is clear evidence that this is the case; Packer, in prep.). Clearly, solitary cleptoparasites do not suffer such inhibitory influences.

H. ligatus has been the subject of more hours of field research than any other New World halictine species (for summaries of this information see Michener and Bennett, 1977, and Packer, in prep.). Most studies have been of temperate populations and not one author has mentioned trap-lining or possible cleptoparasitism within the species. Detailed field work by the author in Ontario during 1983 and 1984 would certainly have showed up the presence of this behavior unless it were extremely rare. Observations involving hundreds of marked bees were carried out in these two years and no behaviors consistent with cleptoparasitism were ever observed. There is reason to believe that the form of intraspecific cleptoparasitism described here may be restricted to subtropical and tropical climes. This is because only where the colonies are continuously brooded and multivoltine is it probable that newly emerged cuckoo individuals will be able to find nests that are at the reproductive phase of colony development. Cleptoparasites in temperate populations would require different behaviors. If they were of the gyne generation they would have to remain inactive until the emergence of workers in other nests, otherwise their ovipositions would result in workers with reduced reproductive success. Cleptoparasites of the worker generation would have great difficulty in entering active summer nests because of their comparatively small size.

"Lost" bees are frequently mentioned in the sweat bee literature. It is possible that such individuals are not lost, but represent a cleptoparasitic subpopulation. Collections of such individuals should be made in order to assess their levels of ovarian development. If they are more fecund than other individuals flying at the time this would be evidence that they are indeed cleptoparasites. Observations of marked individuals would verify such claims; such detailed investigations are badly needed.

The cleptoparasitic individuals of *H. ligatus* parasitize the nests of conspecifics. They seem to possess no special adaptations to parasitic behavior other than the ability to detect and trap-line host nests and recognize nests that should be preferentially parasitized. Secretive oviposition and techniques for assuring entry into defended nests are almost certainly abilities that are possessed by nonparasitic individuals in this population: egg-laying workers and returning young gynes respectively (Packer and Knerer, 1986a). Returning young gynes often have to fight their way past bees at entrances to their natal nest. The ability to forcibly re-enter natal nests could have served as a preadaptation to cleptoparasitic behavior.

Two alternative strategies will not co-exist in a population unless they are, on average, equally successful (Brockmann et al., 1979). The advantage to pursuing a cleptoparasitic strategy at this locality is easy to see. Knights Key is a coral island and *H. ligatus* foundresses have to locate earth filled fissures in the bedrock that are hidden beneath the shallow soil surface. Many unsuccessful nest initiation attempts probably result causing these females to be at risk from ant predation for a prolonged time. Although not investigated in any detail, it seems certain that mortality during the early stages of nest initiation are much higher in this population than in that studied in Ontario (Packer, in prep.). Under these circumstances, cleptoparasitism may be particularly favored.

Because most cleptoparasitic species are closely related to their hosts, it has been suggested that sympatric speciation must have been involved in their origin. A hypothesis that does not invoke sympatric speciation has been suggested by Wilson (1971). If speciation occurs as a result of geographic isolation and the barrier between the newly diverged populations is removed it is possible that one species could evolve to be parasitic upon its recently diverged sibling. It should be noted that parasitic behaviors could have arisen in the ancestral population or in either or both of the daughter populations before becoming fixed in one of them when they became sympatric once more. In this regard it is worth noting that many bees live in small, localized aggregations that would facilitate such a mechanism. Additionally, this study was carried out on one of a series of small islands—the Florida Keys. It is interesting to speculate that the observations made here represent the first stages in the incipient differentiation of a cleptoparasitic species.

What effect this parasitic strategy has upon the social organization of *H. ligatus* at this site will depend upon the nature of the basis of cleptoparasitic behavior. If this is a genetic strategy then it is likely that a proportion of the female offspring of cuckoo mothers will also be parasites (the exact proportion, clearly, depending upon the mode of inheritance). The remaining female offspring of cuckoo mothers, those not manifesting cuckoo behavior themselves, should presumably start their own nests or become laying individuals in the host colony. In the latter instance they would decrease the mean coefficient of relatedness among the females in the nest. The powers of dominance exhibited by *H. ligatus* foundresses at Knights Key are reduced in comparison to more northern populations. It will be argued elsewhere that this may be the result of a reduced degree of relatedness among nestmate females, clearly the presence of cuckoo offspring may play a part in this. It is too early for any precise statements on the exact nature of cleptoparasitism or the effect of cuckoos on sociality to be made: more field observations on the frequency of cleptoparasitism and the fate of cuckoo-laid eggs are required.

Eickwort and Eickwort (1972) have described three types of host nest entry in *Sphecodes.* 1) Sneak attack, in which the cleptoparasite enters the nest while the rightful occupant is absent; this is generally restricted to attacks on solitary host species or social species during the spring (often monogynous) phase. 2) Colony attack, in which the intruder has to force its way into the nest, fighting and killing the occupants as it does so; this has been described for *Sphecodes monilicornis, S. minor* and *S. gibbus* attacking *Lasioglossum* (*Evylaeus*) *malachurum, L.* (*E.*) *cinctipes* and an unnamed species of *Halictus* respectively. 3) Host impersonation, in which the parasite gains entry to the nest as if it were a member of the host colony and elicits few, or no aggressive responses from the hosts that it encounters. This entry technique was described for *Microsphecodes kathleenae* entering the nests of its eusocial host *Lasioglossum* (*Dialictus*) *umbripenne* (Eickwort and Eickwort, 1972).

S. pimpinellae has been recorded as eliciting unusual escape responses in its host *Augochlorella striata* (Ordway, 1964). This should perhaps be regarded as a fourth type of entry type—a host repellant strategy.

The cuckoo-like behavior exhibited by some individuals of *H. ligatus* at Knights Key would seem to be a more primitive and generalized strategy than any of these. They do not sneak into empty nests or engage in fatal battles in the host colony nests. Rather, they seem to enter nests, cause confusion and probably sneak in an oviposition or two during the ensuing melée, this being facilitated by the comparatively anarchic social organization of the host at this locality.

This paper describes the first recorded example of cleptoparasitism between conspecifics of a social insect. It indicates that, in this instance at least, the amount of behavioral modification required for this strategy to be successful may be quite small.

ACKNOWLEDGMENTS

The author would like to thank Dr. Richard Fisher and two anonymous referees for commenting upon an earlier version of the manuscript and thereby greatly improving the final version. Financial support for field work was obtained from an NERC NATO scholarship and an NSERC operating grant awarded to G. Knerer. The field assistance of Michelle Smith is very gratefully acknowledged. The paper was written while the author was supported by an Ontario Graduate Scholarship and publication charges were borne by a NSERC grant to Professor G. Knerer.

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Received October 2, 1985; accepted January 3, 1986.

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J. New York Entomol. Soc. 94(4):467–471, 1986

A REVISION OF THE *EUPREPES* SPECIES GROUP OF *COSMIOCRYPTUS* (HYMENOPTERA: ICHNEUMONIDAE)

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Abstract.—*Cosmiocryptus* of the *euprepes* group are red, black, and white ischnines with the ovipositor compressed, vertical ridges on the ovipositor tip, and the female front tibia inflated. *Cosmiocryptus euprepes* (Porter), new combination, inhabits gallery forests near Buenos Aires, Argentina. *Cosmiocryptus eugrammus,* new species, frequents the northwest Argentine Subandean Desert. It differs from *euprepes* in having the mesoscutum uniformly black, the mesosoma without red markings, the first flagellomere more slender, and the propodeal cristae weakly subcrescentic or subcuneate.

The species here discussed belong to the subtribe Ischnina of the geline tribe Mesostenini (as defined by Townes, 1969).

Cameron (1902) proposed *Cosmiocryptus* for a single new species (*C. violaceipennis*) from the Peruvian Coastal Desert. Recent workers (Porter, 1967; Townes, 1969) have viewed *Cosmiocryptus* as a synonym of *Trachysphyrus* Haliday (1836). Subsequent accumulation of more than 100 undescribed species in *Trachysphyrus* (s.l.) has revealed enough diversity to justify recognition of several new genera and resurrection of *Cosmiocryptus* from synonymy.

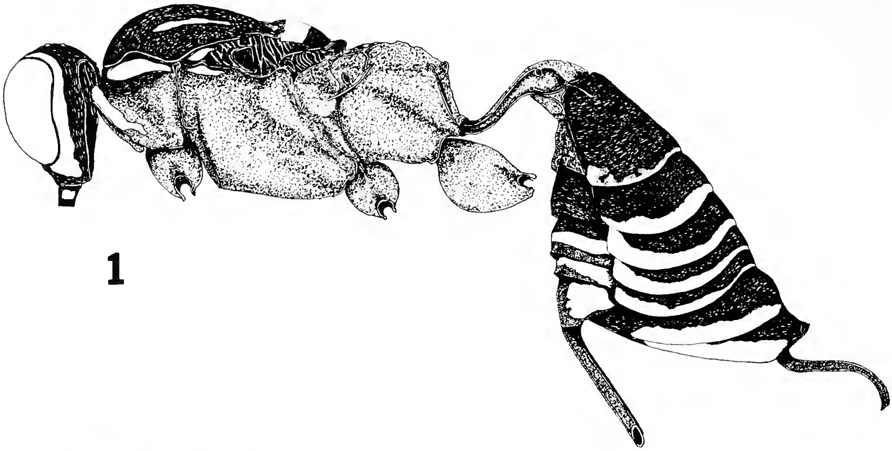
Cosmiocryptus now is regarded (Porter, 1985b) as a large South American genus related both to *Trachysphyrus* and to *Chromocryptus* Fitch. From these, it differs because the axillus vein runs close to the anal margin of the hind wing, the base of the first gastric tergite has no strong lateral expansions, the mediella is often moderately arched rather than straight, and the second gastric tergite never is both coarsely and densely punctate (diagnosis polythetic).

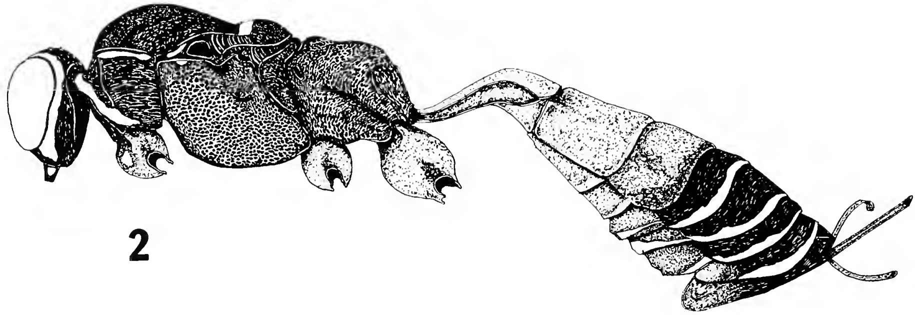
Both *Trachysphyrus* and *Cosmiocryptus* remain heterogeneous and probably paraphyletic taxa. *Chromocryptus* (Porter, 1985a) is regarded as a monophyletic unit that includes only the North American *C. planosae* (Fitch) and several very similar species from the southern United States, Mexico, and South America.

One of the most apomorphic *Cosmiocryptus* is *Trachysphyrus euprepes* Porter (1967), which inhabits subtropical gallery forest near Buenos Aires, Argentina. In this species the ovipositor is compressed and the female front tibia inflated, features which suggest parasitism of lepidopterous larvae that bore in stems or twigs. A specifically distinct but similarly modified *Cosmiocryptus* has now been discovered among Malaise trap samples from the northwest Argentine Subandean Desert. Herewith, I describe the new taxon, give additional locality data for *C. euprepes,* and furnish a revised diagnosis of the *euprepes* species group.

DIAGNOSIS OF THE *EUPREPES* SPECIES GROUP

Flagellum not flattened below toward apex, its first segment 5.9–7.3 as long as deep at apex; clypeus bluntly subpyramidal in profile, its apical margin slightly convex





Figs. 1, 2. 1. *Cosmiocryptus euprepes,* female. Body in lateral view, showing habitus and color pattern. 2. *Cosmiocryptus eugrammus,* female. Holotype. Body in lateral view, showing habitus and color pattern.

and without teeth or tubercles; malar space 0.8–0.9 as long as basal width of mandible; front tibia in female stout and inflated; pronotum with dorsal margin a little inflated and the submarginal groove indistinct; epomia strong in pronotal scrobe, not prolonged or modified; mesoscutum with the well defined notauli reaching 0.3–0.6 its length and with its surface densely punctate, mat to extensively shining; mesopleuron finely but often rather strongly reticulately wrinkled; wing with areolet moderately large, a little high and narrow, its intercubiti strongly convergent above, and with second abscissa of radius 0.5 as long as first intercubitus, as well as with the second recurrent a little reclivous and slightly outcurved on upper 0.5, disco-cubitus weakly angled, ramellus present or absent, mediella gently arched, axillus close to anal margin of hind wing; propodeum short and high to moderately elongate, its apical face discrete and abruptly declivous, its cristae weakly subcuneate to broad and strongly subligulate, its surface largely with strong reticulate wrinkling; first gastric tergite with a low and flange-like lateral expansion at base of petiole, postpetiole 1.1–1.5 as wide apically as long from spiracle to apex, ventro-lateral carina sharp throughout, dorsolateral carina traceable throughout and strongest on postpetiole, dorsal carinae detectable and best developed on postpetiole, and with strongly granular micro-reticulation on the mat postpetiolar surface; second gastric tergite dully shining or mat with abundant, well separated to semiconfluent (but largely discrete), shallow, small to medium sized punctures which emit short setae that mostly approach, equal, or exceed the length of their interspaces; ovipositor with sheathed portion 0.6–0.8 as long as fore wing, straight, strongly compressed, with very low nodus and tiny nodal notch, with dorsal valve on tip showing a gently convex taper between notch and apex, and with ventral valve on tip vertically cut by fine and well spaced ridges.

KEY TO SPECIES OF THE *EUPREPES* GROUP

1. Propodeum and thoracic pleura extensively red; mesoscutum with a pair of white discal stripes along notauli; hind tarsus partly white; first flagellomere 5.9 as long as deep at apex; mesoscutum extensively shining; propodeal cristae strong and broadly subligulate; second gastric tergite with well separated punctures .... *C. euprepes* (Porter)
– No red on mesosoma; no white along notauli or on hind tarsus; first flagellomere 6.9–7.3 as long as deep at apex; mesoscutum mat; cristae weakly subcuneate; second gastric tergite punctures adjacent to subconfluent .... *C. eugrammus,* n. sp.

Cosmiocryptus euprepes (Porter), **New Combination**
Fig. 1

Trachysphyrus euprepes Porter, 1967:101. Type locality, Punta Lara in Buenos Aires Province, Argentina. Holotype female, American Entomological Institute.

New material examined. Argentina (La Balandra in Buenos Aires Province, 27.XI.1968, C. Porter), 2 females, in C. Porter Collection.

Habitat notes. My specimens were swept from herbaceous undergrowth in subtropical gallery forest along the Río de la Plata near La Plata city.

Cosmiocryptus eugrammus, new species
Fig. 2

Description. Female. Antenna black with pale brown on scape below and with white above from apex of fifth through base of ninth flagellomere; head and mesosoma black with the following white: spot on first maxillary palpomere; large blotch on base of mandible; large blotch on clypeus; orbital ring which is interrupted at bottom of eye anteriorly but which posterio-ventrally reaches far into malar space; band on most of front pronotal margin, except toward lower corner and except for a dusky area on meson of collar; narrow band on dorso-lateral margin of pronotum; most of tegula; tiny spot on subalarum; and anterior 0.4 of scutellum; first and second gastric tergites pale red with slight dusky staining; third tergite pale red with black on apical 0.4 and with apical rim narrowly brownish; fourth tergite black with a very broad white apical band; fifth to seventh tergites black with broad but dorsally narrowed or even briefly interrupted white apical bands; and eighth tergite black (becoming brownish ventrad) with white on dorso-lateral 0.5 of apical margin and also very narrowly on dorsal apex; legs pale red (tibiae and tarsi duller), front coxa extensively blackish with a dorso-anterior white blotch basad, mid coxa sometimes black toward base, front and mid trochanters blackish above, apex of hind tibia slightly dusky, hind tarsomeres dusky; and wings hyaline. Length of fore wing 6.0–6.6 mm.

Clypeus rather high and bluntly to a little sharply asymmetrically pyramidal in profile, its apical margin a little convex. Malar space 0.85–0.92 as long as basal width of mandible. Temple 0.5 as long as eye in dorsal view.

Front tibia stout and inflated. Mesoscutum with notauli narrow and well defined for 0.3–0.5 its length, its surface mostly mat with small, subadjacent to adjacent or reticulately confluent punctures that grade meso-apicad into strong but fine reticulate wrinkling. Mesopleuron with speculum largely reticulo-punctate and with surface otherwise finely but strongly reticulo-rugose. Ramellus present.

Propodeum a little elongate, its basal face gently sloping apicad, its well differentiated apical face steeply declivous and only 0.6–0.7 as long as basal face, the cristae broadly subcuneate but inconspicuous. Postpetiole 1.1–1.5 as wide apically as long from spiracle to apex, its surface mat with strongly granular micro-reticulation. Second gastric tergite mat with granular puncto-reticulation, its rather small and shallow punctures mostly adjacent to semiconfluent and emitting short setae which in general slightly exceed the length of their interspaces. Ovipositor with sheathed portion 0.6–0.7 as long as fore wing; straight, rather slender, strongly compressed; dorsal valve with a gradual, slightly convex taper between notch and apex; ventral valve on tip with well spaced, sharp, nearly vertical ridges.

Male. Unknown.

Holotype. ♀, Argentina (Yacochuya near Cafayate in Salta Province, 1,950 m, 1–15.III.1969, in Malaise trap, L. Stange, A. Terán and A. Willink), in collection of the Fundación e Instituto Miguel Lillo.

Paratypes. 3♀♀, same locality and collection data as holotype, 1–15.III.1969, 16–31.III.1969, 16–31.XII.1969. Deposited in Florida State Collection of Arthropods, American Entomological Institute and C. Porter Collection.

Relationships. This species closely resembles *Cosmiocryptus euprepes* (Porter) in its swollen female front tibia and compressed ovipositor with weak nodus and nearly vertical ridges on the ventral valve near apex. It may be distinguished from *C. euprepes* by the following combination of characters: no red on mesosoma, no white stripe along notaulus, first and second gastric tergites without white apical bands, third tergite red basally, no white on hind tarsus, first flagellomere 6.9–7.3 as long as deep apically, notaulus only 0.3–0.5 the length of mesoscutum, mesoscutal surface largely mat with adjacent to reticulately confluent punctures, speculum mostly puncto-reticulate, ramellus developed, propodeal cristae weak and subcrescentic or subcuneate, apical face of propodeum definitely shorter than basal face, postpetiolar granulation stronger, and second gastric tergite with adjacent to subconfluent punctures.

Habitat notes. Like so many other *Cosmiocryptus, C. euprepes* has been taken only by Malaise trap. The type locality is a permanently watered ravine located near 2,000 m in an ecotone between the Subandean and Prepuna Biomes, as well as containing some relict biota of Chaco or wet forest affinities (Porter, 1975). Two Malaise traps were left at this site, one "across an irrigation ditch beneath a *Prosopis nigra* . . . with *Salix, Trichocereus, Cestrum,* and *Nicotiana* in the vicinity" and the other "at the foot of a rocky slope with *Trichocereus, Bulnesia, Prosopis, Caesalpinia,* and other desert growth" (Stange, Terán, and Willink, 1976:89–90).

Specific name. Eugrammus is the latinized masculine singular of the Greek adjective *eugrammos,* "well drawn, with elegant lines."

COLLECTIONS

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ACKNOWLEDGMENTS

This work was done under the author's current National Science Foundation Grant (BSR-8313444). Mr. Thomas J. O'Neill of Fordham University prepared the illustrations. Fieldwork in Argentina was accomplished in collaboration with Dr. Abraham Willink and Ing. Agr. Arturo Terán of the Fundación e Instituto Miguel Lillo. Support for this and similar projects also came from the Florida State Collection of Arthropods, of which I am a Research Associate.

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Received December 20, 1985; accepted April 17, 1986.

J. New York Entomol. Soc. 94(4):472–479, 1986

BIONOMICS OF CREPUSCULAR BEES ASSOCIATED WITH THE PLANT *PSOROTHAMNUS SCOPARIUS* (HYMENOPTERA: APOIDEA)

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Abstract.—Information on the nesting biology is reported for *Caupolicana ocellata* Michener (Colletidae: Diphaglossinae) and *Martinapis luteicornis* (Cockerell) (Anthophoridae: Eucerini). These species collect pollen from *Psorothamnus scoparius* (Gray) Rydberg (Leguminosae). Nests of both species were found near one another close to the Willcox playa in southeastern Arizona. Details of nest architecture, provisioning and a description of the egg of *Martinapis* are presented. This information is compared and contrasted with related bees. Also provided is casual information on the early matinal flight periods of the two species and of *Caupolicana yarrowi* (Cresson).

We present here data primarily on the nesting biology of two large-bodied, distantly related, crepuscular bees associated with *Psorothamnus scoparius* (Gray) Rydberg (=*Dalea scoparia*) (Leguminosae) (kindly identified by Rupert C. Barneby, New York Botanical Garden). Michener (1966) previously briefly described the nest of one, *Caupolicana ocellata* Michener (Colletidae: Diphaglossinae). We give additional information, and are able to compare it with what is known of other Diphaglossinae because of a recent treatment of the subfamily by Rozen (1984). Nests of *Martinapis luteicornis* (Cockerell) (Anthophoridae: Eucerini) (and of the other two species in the genus) were undescribed.

This paper also provides some information on the daily flight activity and floral relationships of these bees because apoidologists have been interested in such matters, especially in relation to large-bodied crepuscular bees from southeastern Arizona and adjoining regions (see, for example, Linsley and Cazier, 1970; Linsley and Hurd, 1959; Michener, 1966; Zavortink and LaBerge, 1976).

Although we had collected both species at 4 miles east of Willcox, Cochise County, Arizona, for several years, we did not discover and excavate nests until August 29 and 30, 1985. Zavortink and LaBerge (1976) investigated the daily activity of *Martinapis luteicornis* at Willcox (and elsewhere), but the occurrence of *Caupolicana ocellata* there apparently represents a westward extension of its recorded range (Michener, 1966).

Specimens of adults and samples of cells of both species are in the collections of the American Museum of Natural History.

DESCRIPTION OF AREA

The nesting area (Fig. 1) of the two species bordered the Willcox playa in a sand dune region that extended for more than a mile in all directions. The dominant large plants that stabilized the dunes were mesquite and the pollen plant, *Psorothamnus* *scoparius,* a woody shrub that grew in clumps intermixed with the mesquite. *Baileya pleniradiata* Harv. & Gray and other low-growing herbs were also abundant, providing a 10–30% surface cover. Cattle and small mammals, including jack-rabbits, cottontails and coyotes, trod the ground. Vegetation did not shade nest entrances.

The fine, even-grained sandy soil contained little organic material except for a few small roots and no stones or rocks, from the surface to the lowest level excavated—about 1.5 m down. Generally loose on the surface because of livestock, the soil became slightly compacted a short distance below, so that at the cell level, we could usually excavate it in clumps that, if handled carefully, would not break. The sandy soil was faintly moist at the cell level. The ground was highly absorbent to rain water, and during high winds, surface sand blew extensively.

At the time of our observations *Psorothamnus scoparius* and *Baileya pleniradata* were in maximum flower, but only a few floral clusters of mesquite still attracted Hymenoptera. *Nama,* though not abundant, was scattered and in full bloom. Because of the profusion of blossoms, a rich assortment of adult bees was active, including more than 16 genera of solitary and social forms, and 7 genera of cleptoparasitic ones.

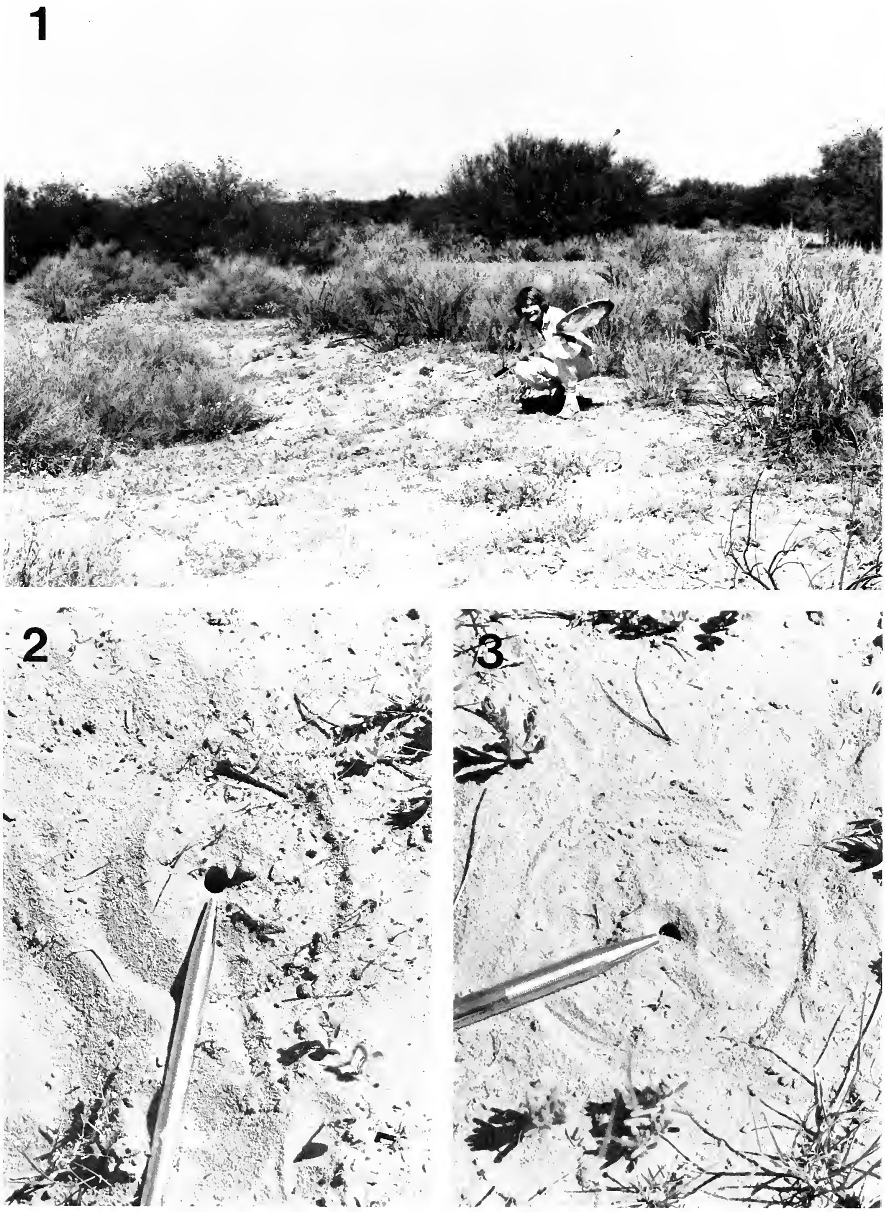
DAILY FLIGHT ACTIVITY AND POLLEN PLANT ASSOCIATIONS

We made casual observations on flight periods only in the morning. The occurrence of these two species on the flowers of *Psorothamnus scoparius* on August 24, 29, and 30 was evident at 5:30 a.m., as were adults of *Caupolicana yarrowi* (Cresson). At that hour, we saw or heard only these three species, but *Bombus sonorus* (Say) and a bembycid *Bembix dentilabris* Handlirsch (kindly identified by Arnold S. Menke, Systematic Entomology Laboratory, U.S. Department of Agriculture) started visiting flowers between 5:45 and 6:00 a.m., Mountain Standard Time. Sunrise over the eastern mountains occurred at 6:15 a.m. *Martinapis* was most abundant, in that several adults visited each clump of blooming *Psorothamnus* most of the time until 7:30 a.m. Zavortink and LaBerge (1976, table 1) gave similar but more complete data on flight times for this species from the same general locality. *Caupolicana ocellata* was much less common, and *C. yarrowi,* uncommon in that we saw only 4 or 5 adults between 5:30 and 8:00 a.m. on August 30.

We observed *Martinapis luteicornis* and *Caupolicana ocellata* collecting pollen solely from *Psorothamnus scoparius.* However, Zavortink and LaBerge (1976) provided substantial data demonstrating *M. leuteicornis* as polylectic, and Michener (1966) associated *C. ocellata* with *Dalea lanata* in Kansas. We captured a single female of *C. yarrowi* on *Psorothamnus* but it carried no pollen. This species forages from a wide variety of plants according to Michener (1966) and Linsley and Cazier (1970).

DESCRIPTION OF NESTS

Caupolicana ocellata. A single nest entrance (Fig. 2) occurred on a low rise, 1 m from the closest clump of the food plant, *Psorothamnus scoparius.* Not situated near any obvious marker on the ground, it was a circular hole, 7.0 mm in diameter, without a tumulus. The main burrow (Fig. 4), 8.0–9.0 mm in diameter, descended vertically without turning in contrast to the meandering main tunnel of *Martinapis*



Figs. 1–3. 1. Nesting site of *Caupolicana ocellata* and *Martinapis luteicornis* 4 miles east of Willcox, Arizona. Barbara L. Rozen at nest entrance of *Caupolicana*; nests of *Martinapis* near mesquite trees in middle ground. 2. Nest entrance of *Caupolicana ocellata* showing circular opening. 3. Nest entrance of *Martinapis luteicornis* showing opening with lower side flattened. Circles around entrances were created by our placing plastic drinking glasses over openings to capture nesting females.

luteicornis. It was open (without fill or plug), lacked an entrance vestibule, but seemed to widen slightly at its terminus at a depth of 84 cm. Its walls were moderately smooth, uncoated, and readily absorbed a droplet of water.

A single open lateral (Fig. 4), 8.0–9.0 mm in diameter, extended 17 cm from near the bottom of the burrow to a partly provisioned open cell. It gradually rose 6 to 7 cm from its junction with the main burrow and then curved abruptly downward to join the open cell. Hence the path of the lateral was similar to but more extended than that of the lateral of the related *Ptiloglossa arizonensis* (Rozen, 1984, figs. 4, 5). Laterals were filled with soil after cell completion and oviposition, so that they were indistinguishable from the substrate.

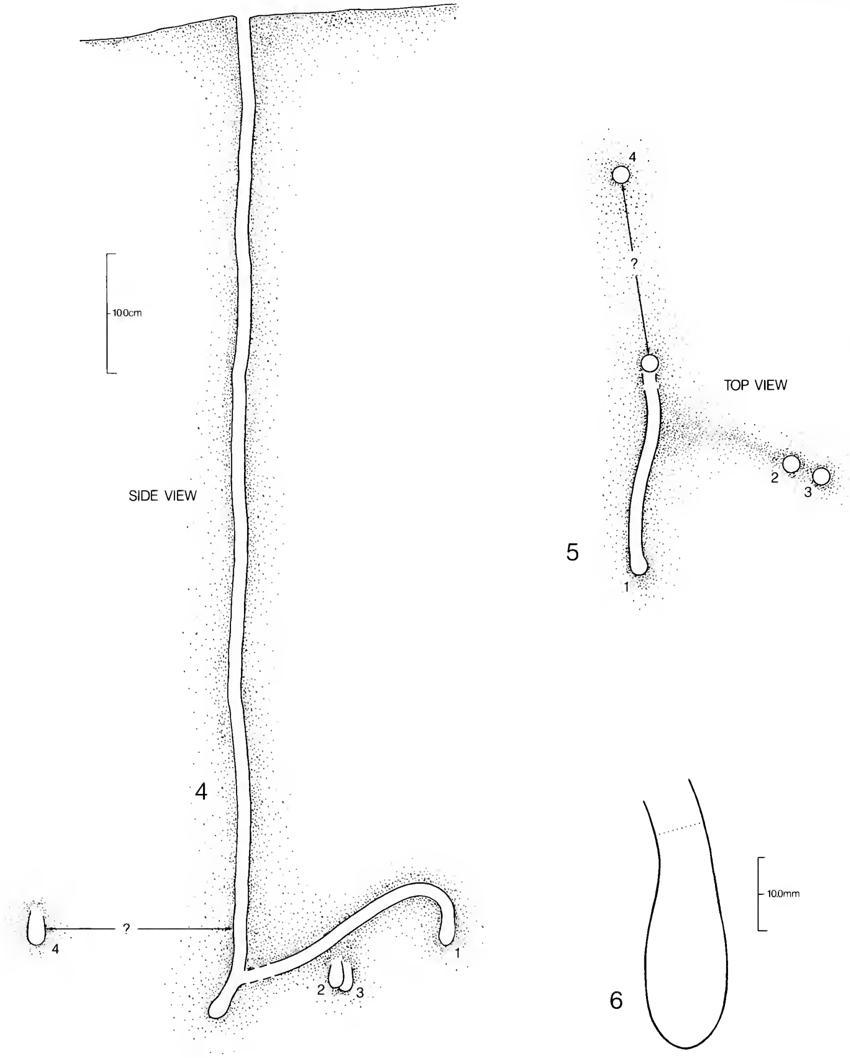
We associated four cells with this nest (Figs. 4, 5), but accidentally destroyed one before we could study it. The three other cells were vertical. The open cell was at a depth of 76 cm, the other two completed cells, at 80 cm, and the destroyed cell, at approximately the same level. The two completed cells were 14.0 and 17.5 cm from the main tunnel and were in a direct line with it, so that a single lateral may have led to them. The order of cell construction in this nest seemed to be from lower levels up, as completed cells were deeper than the open one.

Cells were 10–11 mm in diameter (three measurements). One measured 23 mm long from its lowest point to where it started to bend toward the lateral (Fig. 6), and another was clearly more than 20 mm long. Although none was measured with the closure in place, cells were obviously elongate. As has been discussed elsewhere (Rozen, 1984), the upper limit of diphaglossine cells must be identified by the closures because the upper part of the cell (neck) bends toward the lateral in most if not all genera. Observations on closures of *Caupolicana ocellata* were not possible.

All cells (including the one destroyed) had a conspicuous cellophane-like, waterproof lining of semitransparent material that closely adhered to the wall and that, at least in one case, extended into the neck where the diameter was 7.0 mm (Fig. 6). The coating was similar to that associated with other diphaglossine cells. The cell wall beneath was very smooth and gave no indication of having been masoned or hardened.

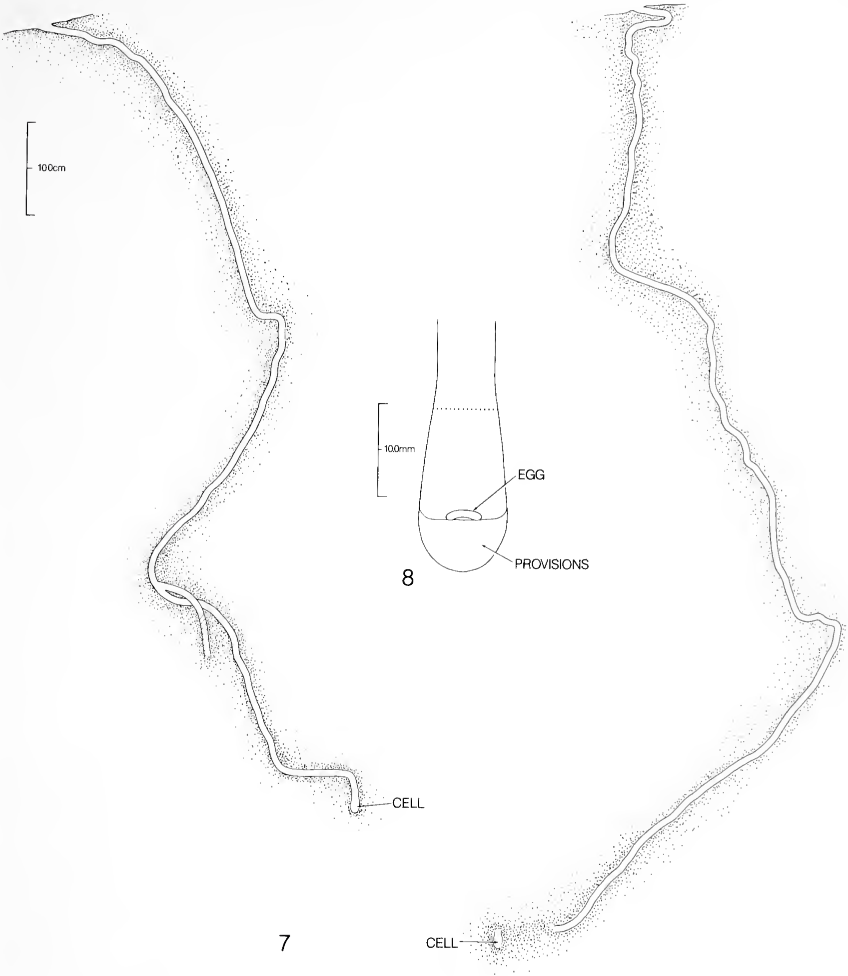
Completed cells were provisioned with copious liquid (presumably nectar) as evidenced by the abundant wet stain in the substrate when cells were accidently punctured. The bright, reddish orange pollen apparently settles to the bottom of the liquid, because most of the pollen remained in the linings of the broken cells. Hence the consistency of the provisions, at least in the early stages of larval development, appeared similar to that of *Ptiloglossa* (Rozen, 1984). The open cell had been provisioned with a small amount of viscous liquid of pollen and presumably nectar. These provisions flowed only slightly when the cell was tilted after removal. We removed a single larva, intermediate in stage, from one cell. Cocoon construction and defecation, matters of considerable variation and interest in the subfamily, remain unknown.

Martinapis luteicornis. We discovered two nest entrances, both without tumuli and each occupied by a single female (captured), about 10 meters apart and about 50 meters from the nest of *Caupolicana ocellata,* described above. The entrances (Fig. 3) were flat on the lower side as a result of the main burrows entering the loose sand surface at a 20° angle from the horizontal. Tunnel walls were moderately smooth (less so than those of the cells), nonwaterproof, unlined and seemingly unworked.



Figs. 4–6. 4. Nest of *Caupolicana ocellata,* side view. 5. Same, top projection. 6. Empty cell of *Caupolicana ocellata,* side view; dotted line indicates upper limit of waterproof lining. Scales refer to Figures 4 and 5, and 6, respectively.

Neither tunnel contained a vestibule. One tunnel gradually turned downward and the other turned back on itself and then descended in a meandering fashion (Fig. 7). Each main tunnel, 6–7 mm in diameter, was open, unplugged, and descended in an erratic, meandering path. The tunnel of one nest branched at a depth of approximately 60 cm. One ramus turned downward, became filled with sand as compact as the substrate and was lost after descending another 10 cm. The other ramus remained



Figs. 7, 8. 7. Two nests of *Martinapis luteicornis,* side view. 8. Composite diagram of cell of *Martinapis luteicornis,* demonstrating shape and position of egg on provisions, but not cell closure; dotted line indicates upper limit of waterproof lining. Scales refer to Figures 7 and 8, respectively.

open and continued on an erratic downward path. At an approximate depth of 84 cm it became horizontal (or nearly so) for a short distance, then abruptly bent downwards, and opened into an open cell (Fig. 7) partly provisioned with bright red-orange, mealy moist pollen. The tunnel of the other nest did not branch and meandered downward to a depth of approximately 100 cm, where it was lost. A single vertical cell containing an egg and provisions was discovered at the same level within 10 cm of the terminus.

We associated one cell with each nest. We found moist pollen in some of our excavated soil from the deeper levels of the second nest, perhaps suggesting that a nest normally consists of more than one cell, that cells are far apart, and that laterals leading to them are filled and untraceable. It seems unlikely that such deep nests would have only one cell, although both *Melissodes pallidisignata* Cockerell (Thorp and Chemsak, 1964) and *M. rustica* (Say) (Clement, 1973) construct single-celled nests.

As is characteristic of most eucerine cells, the two cells (Fig. 8) were radially symmetrical, vertical and possessed a very smooth wall coated with a shiny, transparent lining, waterproof when tested with a droplet of water. The lining in one cell extended 17 mm from the bottom of the cell to the cell entrance. Cells were 8.5 and 9.0 mm in maximum diameter, and one was 17–18 mm long. The top of the cell containing the egg had been scraped away during excavation, so that information regarding cell closure is unknown. In general the cells had an elongate shape characteristic of other eucerines that we have investigated (Rozen, 1964, 1969, 1974, 1983). A special cell wall was not clearly defined although the substrate next to the lining may have been slightly harder than elsewhere.

The homogeneous, non-layered, brightly colored, mealy moist provisions (Fig. 8) in the completed cell emitted a cheesy odor and contained many bubbles, a suggestion of fermentation. The food occupied the bottom of the cell to a central depth of 5.5 mm, but its surface curved upward at the wall. The single curved egg, 3.4 mm long and 0.7 mm in maximum diameter, was cylindrical and rounded at both ends. The chorion was yellowish, opaque, and dull due to microscopic external sculpturing. Both ends of the egg rested on the provisions near the center of the cell, while the arched middle part rose from the food surface. The egg closely resembled that of *Svastra obliqua* in shape, color, texture, and placement (Rozen, 1964).

DISCUSSION AND CONCLUSIONS

Information on *Caupolicana ocellata* agrees with what is known about the nesting biology of diphaglossine bees (Rozen, 1984). The vertical, heavily lined, curved cells are a striking feature of all diphaglossines. Further studies need to be carried out on *Caupolicana* to elucidate such intriguing matters as the type of cell closure, characteristics of the upper end of cells, the nature of the provisions, larval feeding habits, defecating habits, and fate of the cell lining at time of defecation and cocoon spinning.

Similarly, what we now know of the nesting habits of *Martinapis luteicornis* corresponds closely with those of other eucerines (Bohart, 1964; LaBerge and Ribble, 1966; Linsley, MacSwain, and Smith, 1955; Mathewson, 1968; Michener and Lange, 1958; Rozen, 1964, 1969, 1974, 1983; Sakagami and Usui, 1976; Thorp and Chemsak, 1964). Most members of the tribe construct elongate, radially symmetrical, vertical cells with round bottoms. The provisions typically emit a cheesy odor, and the egg chorion is often (if not always) dull. For *Martinapis,* we need a clearer understanding of the number of cells to a nest, the overall nest architecture, and information on fecal deposition and cocoon construction.

Although a number of genera of cuckoo bees occurred in the area, none seemed to be active in the morning hours when these two species were flying, and we certainly recovered no cleptoparasitic eggs or larvae from the nests.

ACKNOWLEDGMENTS

We wish to thank Wallace E. LaBerge, State Natural History Survey Division, Illinois Department of Energy and Natural Resources, for critically reviewing the completed manuscript.

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Received November 27, 1985; accepted February 28, 1986.

J. New York Entomol. Soc. 94(4):480–488, 1986

ETHOLOGY OF THE BEE *EXOMALOPSIS NITENS* AND ITS CLEPTOPARASITE (HYMENOPTERA: ANTHOPHORIDAE)

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Abstract.—The nesting biology and other aspects of the natural history of *Exomalopsis nitens* (Exomalopsini) are described and compared with the ethology of other members of the genus. This bee nests in walls of cracks in claylike soil in southern California; cells range in depth from 20 to 54 cm. Numerous females use a single surface entrance to the fissures, but each apparently constructs an individual nest in the crack face. Cells are arranged either singly or in series of two and agree in shape and other details with cells of other species in the genus. Provisions are formed into smooth elongate loaves, each supported by a 'foot' at the front. Elongate, curved eggs are deposited on top of the food masses toward the front and feeding larvae crawl around the masses. Fully fed larvae either defecate and pupate immediately, or spin cocoons incorporating fecal material and then enter diapause, depending upon factors not fully understood. The structure of the cocoon differs in certain respects from that of other *Exomalopsis.* An undescribed species of cuckoo bee belonging to the genus *Melanomada* (Nomadini) attacks the host nest by entering just after the *Exomalopsis* females depart to forage, and then depositing eggs in the cell wall. *Melanomada* larvae crawl as they feed and enter diapause without cocoon spinning.

This is the first account of the nesting biology of *Exomalopsis* (*Anthophorisca*) *nitens* Cockerell (Exomalopsini). This species ranges from Santo Tomas, Baja California, Mexico, north to Monterey County, California, and, in southern California, inland to Oak Grove, San Diego County, and the Gavilan Hills, Riverside County. *E. nitens* has also been taken at Bagby, Mariposa County, in the western foothills of the Sierra Nevada (Timberlake, 1980). We also present data on an undescribed species of cuckoo bee belonging to *Melanomada* (Nomadini). This association, considered highly probable before (Rozen, 1984), is now confirmed, but the cleptoparasite was thought to be *Hesperonomada melanantha* Linsley. We will name and describe our species, which is closely related to *H. melanantha,* in a taxonomic revision of *Melanomada.* The monotypic *Hesperonomada* is a junior synonym of *Melanomada* as proposed earlier by Rodeck (1945).

Samples of burrows, cells, cocoons and immature stages are in the collections of the American Museum of Natural History.

NESTING ETHOLOGY OF *EXOMALOPSIS NITENS*

This species nested about 0.5 mile west of Interstate 15 along Indian Truck Trail Road, 12 miles south of Corona, Riverside County, California. R. R. Snelling first discovered the site in 1983, and we made our study on May 22, 24–26, 1985.

Description of nesting area. All nests were in cracks (Figs. 2, 3) in sloping ground on a hillside that was partly covered with clumps of herbaceous plants about one meter high, consisting predominantly of grasses, *Eriogonum fasciculatum,* and *Hemizonia fasciculata* (Fig. 1). The vegetation cast little shadow on the surface entrances to the nests, which were not in areas that would be subject to flooding or man-made disturbances. We found six surface entrances altogether, four within a meter of one another and the other two, 20 cm apart, approximately 30 m away. More than one female used each surface entrance, as is characteristic of other *Exomalopsis,* and we captured a maximum of 12 females coming to or leaving one surface entrance. All surface entrances allowed access to deep crevices that were often closed at the surface. These long, essentially vertical fissures (Fig. 3) penetrated the ground well below where cells were recovered (20–54 cm), ran in various directions, and occasionally interconnected. They presumably resulted from shrinking of the claylike substrate as it lost water with the advancing dry season. The surface entrances (Fig. 2) represented places where surface debris did not obscure the crack, so that the bees, by entering at that spot, were then able to descend into the crevice and construct nests. All the entrances lacked tumuli and turrets. The vertical, uneven opposing faces of a fissure were separated in some places by several centimeters so that females, once in the crack, had available to them much of the two faces in which to start nests. As a consequence, females did not construct composite main burrows as is the case with most *Exomalopsis.*

The fine, claylike soil contained irregularly shaped, small stones that were abundant toward the surface but gradually became less abundant below. At the cell level the soil was moist and difficult to excavate because its sticky nature caused it to adhere to trowels and knives, and we could not easily fracture small soil clumps when we attempted to twist them apart. The soil in many ways was reminiscent of the clayey soil in which *Exomalopsis chionura* Cockerell was also found nesting in vertical fissures (Rozen and MacNeill, 1957).

Description of nests. Nest entrances were scattered along the vertical surfaces of the cracks. One series of five entrances, 20–22 cm below the ground surface, was grouped so that some holes were as close as 2 cm and the greatest distance between any two was 7 cm. Elsewhere entrances were probably more widely scattered, both horizontally and vertically. Although some were found as deep as 54 cm, we suspect that even deeper ones would have been found had we had time to dig deeper.

The entrances in the crack faces were circular, not filled with soil and approximately 3.5–4.0 mm in diameter. The relatively few cells associated with some entrances suggested that a single female was responsible for the tunnel and associated cells. The main tunnel, unfilled, penetrated in a meandering fashion usually more or less horizontally (Fig. 3), but some burrows at greater depths descended almost vertically. Both main tunnels and laterals were 3.3–3.5 mm in diameter (four measurements) and had a non-waterproof wall that generally showed no indication of having been masoned and that was so rough that we could not detect signs of pygidial plate prints. Laterals were filled with soil after completion. Several clusters of cells, presumably nests, were close to the crack wall. One such cluster (Fig. 3) ranged horizontally from 3 to 6 cm from the crack. The largest single nest, still incomplete, contained six cells, and another five cells.

Cells were arranged both singly (Fig. 4) and in linear series of two (Fig. 5) and had the front end always higher than the rear, although the slope of the long axis varied.

Figs. 1, 2. 1. Nesting site of *Exomalopsis nitens,* 12 miles south of Corona, California, showing general vegetation type and R. R. Snelling examining nesting surface. 2. Pencil pointing at surface entrance to nest of *Exomalopsis nitens,* in partly obscured crack extending from lower left hand corner to upper right hand corner of picture.

The cell ceiling was vaulted whereas the floor was flatter, so the cells were not symmetrical around their long axes. Cell length (from rear of cell to middle of closure) ranged from 7.0 to 8.0 mm (five measurements); maximum cell diameter, 4.8–5.0 mm (seven measurements); and diameter of entrance, 2.9–3.5 mm (five measurements), so that the entrance was generally smaller than the burrow diameter. The cell wall did not show definite signs of having been masoned, and was neither harder nor softer than the substrate. The lining was smooth but uneven because of small stones protruding into the lumen. We could not easily peel the somewhat shiny coating from the surface, and it seemed waxlike when scraped with fine forceps. When heated on a hotplate to 700°F, however, the coating did not melt and remained otherwise unchanged.

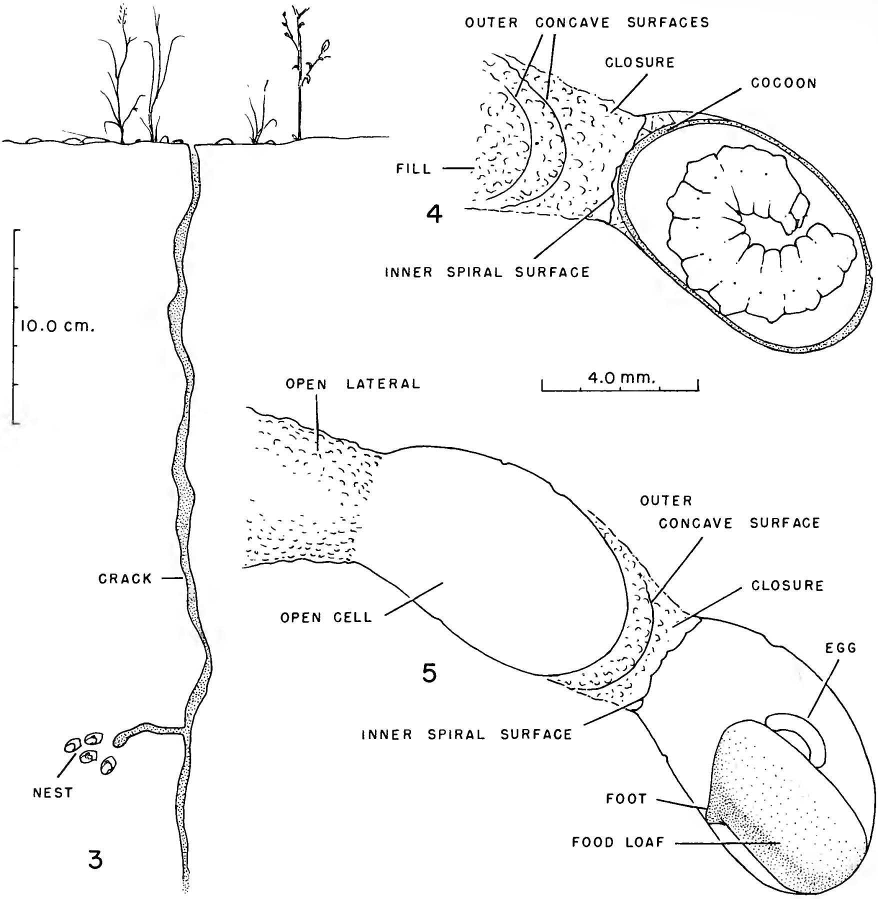
Each cell closure on the inside consisted of a slightly concave spiral of 4 to 5 well defined coils. Where cells connected directly to laterals (Fig. 4), the outside of the closure had two strongly concave, specially worked, smooth surfaces, one in front of the other, imprinted particularly around the periphery by the female's pygidial plate. The space between the two surfaces was filled with soil. Where two cells were in tandem (Fig. 5), a single strongly concave, smooth surface appeared between the spiral closure of the second cell and the rear of the first cell, and the space between the concave surface and the rear of the first cell was filled with soil. The spiral inner and concave outer surfaces absorbed water droplets, although at a somewhat slower rate than freshly broken soil. The pygidial plate embossings on the outer surfaces of the closure suggest that the female uses her pygidial plate to work not only these surfaces but presumably also the cell wall.

Laterals were filled with loose soil after cell closure.

Provisioning. During our excavations, we only observed bees collecting pollen from *Hemizonia fasciculata* (Compositae), but most food loaves and feces consisted of two kinds of pollen, one being three times the diameter of the other. We conclude, therefore, that another pollen source was visited, very possibly *Eriogonum fasciculatum,* which was also blooming adjacent to the nests. Recorded floral visits on specimens we have examined include the plant genera *Calochortus, Malvastrum, Opuntia, Bloomeria, Chlorogalum, Grindelia, Hemizonia, Heteromeles,* and *Clarkia.* at our site it had been taken on *Eriogonum fasciculatum, Hemizonia fasciculata, Raphanus* sp., *Opuntia prolifera, Malvastrum fasciculatum,* and *Calochortus catalinae.* Early in the season (May to early June), females foraged primarily on *Hemizonia* and *Malvastrum.* In late June, foraging switched primarily to *Eriogonum fasciculatum.*

Females transported pollen in a dry state on the large scopae on the hind legs and stored it at the rear (bottom) of the cell as a partly moist, partly dry unshaped mass. Finished provisions (Fig. 5) were shaped into an elongate, homogeneous, semimoist, smooth-surfaced, yellow loaf attached by its rear to the rear of the cell and supported on the floor by a well-formed foot, as typical of most but not all *Exomalopsis.*

Development. White and strongly curved eggs (2.20 mm long and 0.55 mm in maximum diameter, one measurement) (Fig. 5) with a smooth chorion were attached to the top front end of the food loaves, by the anterior and posterior ends. The middle of each egg arched upward so that its venter did not touch the loaf. The anterior of the egg was closest to the cell closure as in all known *Exomalopsis.* Feeding larvae crawled over the food mass, channeling the provisions beneath them. Intermediate



Figs. 3–5. Nest components of *Exomalopsis nitens.* 3. Sketch diagraming relationship of nest to crack, side view. 4. Single cell containing postdefecating larva within cocoon, side view. 5. Two cells in tandem, first one open, second one containing food mass and egg, side view. Scales refer to Figure 3, and Figures 4 and 5, respectively.

stage larvae cradled the now elongate and reduced provisions so that the food no longer touched the cell wall, as seems characteristic of other species in the genus. Fully grown larvae sometimes retained a very small mass of food attached to their venters.

Some mature larvae spun cocoons and others did not. Those that did not pressed their feces as elongate pellets to the rear (bottom) of the cell, so that the fecal material extended part way toward the closure, as illustrated for *Exomalopsis sidae* (Rozen, 1984, fig. 31). They remained active and pupated a few days after completing defecation.

All larvae that spun cocoons diapaused for the season after completing the cocoon.

They usually, if not invariably, started defecating before they had consumed all of their food. In early stages of construction the cocoon fabric consisted of a webbing of gauzelike, fine, white silk with elongate, flattened yellow fecal streaks applied here and there, around the entire inner surface of the cell. However, in early stages of construction, the webbing was so thin as to be nearly invisible, but still several fecal smears were present on top of it rather than on the cell wall. This indicates that silk production commenced synchronously with, or just before, defecation, in contrast to the silk production/defecation timing of other known *Exomalopsis* (see Rozen, 1984). Although in *Exomalopsis nitens* a near synchrony exists, still a conspicuous outer layer of silk was laid down before most of the meconial mass was deposited, as revealed in completed cocoons. Hence the early fecal smears were only a minor part of the entire meconium.

In completed cocoons, the thin outer and inner layers of matted, semitransparent, fine silk sandwiched a thicker, opaque layer primarily of yellow feces consisting of vaculated pollen grains. The combined three layers were roughly 0.1–0.2 mm thick in most places. The outer layer had fine silk strands on the surface, giving it a slightly fuzzy appearance and reducing the surface reflection somewhat; the inner silk layer lacked such fine loose strands and was shiny but crinkly.

With most cocoons, light transmitted through the fabric showed that the front and rear of the cocoon were more opaque because of somewhat thicker fecal layers there. One cocoon had more fecal material at the front end, so that the casing there was approximately 0.5 mm thick, and few fecal deposits elsewhere. Hence considerable variation exists with respect to fecal placements and a larger sample needs investigation.

The incorporated feces gave the cocoon fabric rigidity so that it did not collapse as in *Exomalopsis sidae.* The cocoon shape conformed to the entire cell wall except for the front where the cocoon was rounded and loosely connected to the truncation of the cell closure, as seen in side view (Fig. 4), by fuzzy strands of loose, white silk. Larvae removed from their cells prior to cocoon construction spun malformed cocoons in artificial containers, an indication that the shape of a normal cocoon is determined by the shape of the cell. As in the other Exomalopsini, cocoons of *E. nitens* lacked both opercula and nipples.

Diapausing postdefecating larvae (Fig. 4) were curled, each with its posterior end toward the rear of the cocoon and its curved anterior end toward the front of the cocoon (i.e., cell closure), as in other cocoon-spinning *Exomalopsis.*

Adult activity. Adults flew during the late morning and early afternoon. Both sexes were seen occasionally on the flowers and several males were captured emerging from surface entrances of nesting cracks, although whether these were freshly emerging individuals leaving for the first time or males departing from their overnight sleeping quarters is uncertain. No matings were observed.

Seasonal activity. The presence of larvae starting to spin cocoons before hibernating and of other larvae pupating soon after consuming all their food suggests that this species is both univoltine and bivoltine, at least at this nesting site. In one nest all larvae pupated immediately without spinning cocoons, raising questions as to what factor or factors, external or endogenous, control voltinism.

On the basis of adult specimens, Timberlake (1947) noted that the flight period extends from mid-May to mid-August in southern California.

ETHOLOGY OF *MELANOMADA*

We oberved a number of males and females of the unnamed cleptoparasitic *Melanomada* flying at the nesting site of *Exomalopsis nitens,* first in 1983 and again at the time of nest excavation in 1985. We saw them primarily in the immediate vicinity of the surface entrances rather than widely distributed over the hillside. It was the apparent interest of several females in a crevice that attracted our attention and led to the discovery of the first nest in 1985. Female parasites flew back and forth around and close to entrances and often landed on a stem or rock, more or less facing the entrances. On a number of occasions perched females immediately and swiftly flew into entrances just after a female *Exomalopsis* departed. The occurrence of numerous cuckoo bees examining one nest area for a while and then departing to another suggested that females had already identified various entrances and were patrolling (i.e., trap-lining) from one to another, so as to find one that was 'appropriate' in which to descend. *Melanomada* females may have waited outside the entrances for *Exomalopsis* females to depart so that the cleptoparasites could follow scent trails created by the *Exomalopsis* females as they ascended from their nests along the faces of the crevice. This matter is further explored in the Discussion. During three days of nest digging we saw only one live female *Melanomada* leaving our excavations, a fact suggesting that cleptoparasites do not wait underground for nests to become available for attack.

Like all Nomadinae, *Melanomada* females probably entered still-open cells of their host and inserted their eggs into the cell wall. Egg punctures in the walls of three cells occupied by *Melanomada* larvae were situated almost next to the closures; one was a deep oblong puncture with a raised cell lining on one side, as if the soil had been very moist when the hole was made; another was a raised flap of cell wall still attached to the wall on one side, beneath which was a hole, as has been described for *Melanomada sidaefloris* and *Nomada* (Rozen, 1977).

A number of cell walls had deep irregular holes that suggested that *Exomalopsis* females may have detected and attempted to destroy *Melanomada* eggs by excising them. The shape and roughness of the holes indicated that the *Exomalopsis* females had used their mandibles to dig out the eggs. Among other taxa of host bees attacked by Nomadinae, imperfections in the cell walls indicate that this means of defense against Nomadinae parasites may be broad ranging. In the current study we saw one cell from an active nest that had been filled completely with soil, presumably by the host female, after it had been partly provisioned. This phenomenon has also been noted in nests of other ground-nesting bees (see for example Rozen, 1977, with respect to *Brachynomada*), and may be another mechanism by which host bees eliminate eggs of cleptoparasites.

We found no eggs or first instars of *Melanomada* during our excavations. Feeding intermediate stage larvae were in various positions on the host food loaves, an indication that these larvae crawled as they fed. While feeding, larvae opened widely and then closed their mandibles in a strong biting action in sharp contrast to the feeding action of such Nomadinae as *Protepeolus* that scrape the food with nearly closed mandibles (Rozen, Eickwort, and Eickwort, 1978).

We excavated all larval *Melanomada* while they were still feeding. Those (four) that remained alive in laboratory containers defecated without cocoon spinning and became totally quiescent, all within several weeks of being excavated. The fact that none pupated after defecating and that no pupae were discovered in cells suggests that *Melanomada* is solely univoltine, whereas the host is both univoltine and bivoltine. If this is true, then nests constructed by those *Exomalopsis* emerging as the second generation in a year are unlikely to be attacked (assuming that the *Melanomada* and *Exomalopsis* adults have approximately the same life span). This arrangement may be a mechanism by which the host population recovers during the second generation from the attack of a successful cleptoparasite. Such a mechanism would assure abundant hosts for the next generation of the cleptoparasite.

On the other hand, collection records for adults of this cleptoparasite extend into mid-August and early September. Hence the species may not be univoltine or it may parasitize another species of *Exomalopsis* with a later flight period.

The low adult and high immature population of *Melanomada sidaefloris* (Cockerell) attacking *Exomalopsis sidae,* as reported by Rozen (1984), may reflect that *M. sidaefloris* also has only a single annual generation and was sampled just as the progeny of the first generation were developing, by which time most of the *Melanomada* adults had died.

DISCUSSION AND CONCLUSION

The nesting biology of this species closely parallels that of other *Exomalopsis,* and especially that of *E. chionura* (Rozen and MacNeill, 1957), partly because both species nest in cracks in claylike soil. At first the double outer concave surfaces of the cell closure of *E. nitens* seemed to be a feature unique within the genus, but a further dissection of cells of *E. chionura* preserved 30 years ago in the collections of the California Insect Survey shows that it also had such an arrangement of the closure. Double-faced closures are not, however, found in cell samples of other *Exomalopsis* in the American Museum of Natural History.

As in *Exomalopsis sidae,* some progeny of *E. nitens* spin cocoons in which they diapause, whereas other larvae pupate immediately after defecation and then presumably emerge in the same season. Further study of this matter needs to be undertaken: (1) to determine how widespread it is among other anthophorid bees; and (2) to ascertain whether (as seems most likely at this time) this is a seasonal phenomenon in which progeny developing early in the year pupate, and later progeny spin cocoons; or whether both pupation and cocoon spinning occur synchronously in the nesting population throughout the year.

The structure of the cocoon of *Exomalopsis nitens* differs in some respects from that of other members of the genus. Further and more complete observations on cocoon construction of all species need to be made to test the nature and significance of the apparent differences.

How are the females of *Exomalopsis nitens* able to find their individual nest entrances along the face of the fissure where there is no light, and why do female *Melanomada* wait outside the surface entrances for *Exomalopsis* to depart before they enter? The answers may be interrelated. We suspect that female *Exomalopsis* follow individually distinctive odor trails on their way downward to their nest entrances and that these trails are identified and used by *Melanomada* females in searching out a nest that has just been vacated. (The presence of individually recognizable odor markers may well be the mechanism by which other species of *Exomalopsis* identify their sections of composite nests.) Thus *Melanomada* relies on long range sensory perception (sight) to make certain that a host female has departed and then uses short range sensory perception (olfaction) to track down the recently vacated nest entrance in the dark along the face of the crack. The fact that only one female *Melanomada* was observed escaping from our excavations during three days of digging supports this hypothesis, in that it indicates that *Melanomada* females, once in fissures, do not wait there and search randomly for individual nest entrances.

ACKNOWLEDGMENTS

We acknowledge the support of both the American Museum of Natural History and the Los Angeles County Museum of Natural History. We thank the following specialists who have kindly read this manuscript: Ronald J. McGinley, Department of Entomology, National Museum of Natural History, Washington, D.C. and Marjorie Favreau, Department of Entomology, American Museum of Natural History, New York. Specimens of cells and cocoons of *Exomalopsis chionura* were lent by Jerry A. Powell, California Insect Survey, University of California, Berkeley.

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Received August 29, 1985; accepted November 15, 1985.

J. New York Entomol. Soc. 94(4):489–499, 1986

SUPPLEMENTARY STUDIES ON ANT LARVAE: MYRMICINAE (HYMENOPTERA: FORMICIDAE)

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Abstract.—The larvae of six species of ants in the genera *Acromyrmex, Orectognathus, Oxypomyrmex, Procryptocerus, Rogeria* and *Zacryptocerus* are described. The larva of *Oxyopomyrmex* is characterized for the first time. Included also are references to the larvae of myrmicine ants found in the literature.

In our 1976 memoir we discussed the limited practical utility for myrmecologists afforded by the study of ant larvae: (1) to detect contamination; (2) to distinguish brood from prey of army ants; and (3) to distinguish parasite and host larvae in mixed colonies. Now we can add a fourth: to distinguish the instars in larval development. This seems to be especially important for the students of caste determination. They need to know when a stimulus must be applied to cause (or prevent) differentiation, as well as the kind and/or strength of the stimulus.

We have always described immature larvae when we had them, which was not often, but in this article we are fortunate in having 3 or 4 stages for 4 of the 6 species described. We do not like to call them instars unless certain conditions are fulfilled: an egg ready to hatch will reveal the characters of the first instar; a first instar ready to moult will contain a fully formed second instar; etc.; etc.; until we find a semipupa (=prepupa) which will have all the characters of the last instar except the shape. But such favorable specimens are rarely found; hence we like to get a large number of larvae. We hope that our descriptions will eventually enable students of living larvae to recognize instars by characters other than size.

Acromyrmex introduces another problem for highly polymorphic ants: how to distinguish mature larvae of the smallest workers from the younger instars of the largest workers.

The terms used below for describing profiles and mandible shapes are defined in our 1976 memoir. When we refer below to our own papers we give only the year and sometimes the page.

TRIBE MYRMICINI

Genus *Myrmica* Latreille

Myrmica scabrinodis Nylander & *M. laevinodis* Nylander

Hinton, 1951:155. The larvae of *Maculinea* (=*Lycaena*) *arion* L. [Lepidoptera: Lycaenidae] feed upon the larvae of these ants, consuming them entirely. The larva of *M. alcon* F. (p. 156) also feeds upon the larvae of these ants, sucking out the juices.

TRIBE PHEIDOLINI

Genus *Messor* Forel

Messor aciculatus F. Smith

Onoyama, 1981:630. A table giving the minimum, maximum and mean duration in days of each stage and instar. The means for stages are: egg 19.4, 1st instar 4, 2nd instar 4.6, 3rd instar 19.2, prepupa 4.7, pupa 13.4, total 69.3.

Onoyama, 1982. The 3 instars are to be distinguished by abundance and length of hairs. Instars illustrated in detail.

Genus *Oxyopomyrmex* Ern. André

Profile aphaenogastroid. Body and head hairs very few, short, unbranched, with frayed tip. Labrum small, bilobed. Mandible pogonomyrmecoid, with only one medial tooth; medial surface of base spinulose.

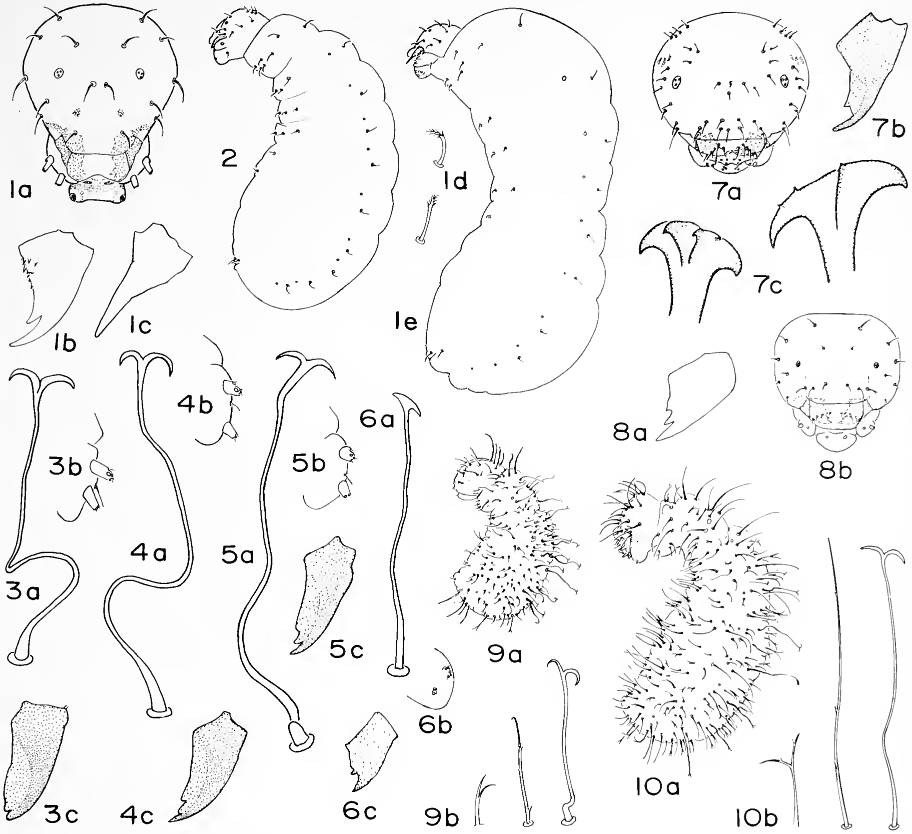
Oxyopomyrmex sp.

Figs. 1, 2

Mature larva. Length (through spiracles) about 2.4 mm. Profile aphaenogastroid. Wing, leg and gonopod vestiges present. Anus posteroventral. Somites indistinct. Spiracles on T2 0.015 mm in diameter; remainder decreasing slightly posteriorly. Integument sparsely spinulose, the spinules minute and isolated. Body hairs few; with stout base and frayed tip. Of 2 types: (1) 0.025–0.05 mm long, with slightly curved tip; 1 on each dorsolateral surface of T1-AV and 4 on venter of AX; (2) 0.012–0.025 mm long, bent as much as 90°, distributed as follows on venter: T1 14, T2-AI 4 each, AII 2, AIII-AX none. Cranium subcircular. Antennae at midlength of cranium, small; with 3 sensilla each. Head hairs 0.025–0.038 mm long, few (about 14), stout, with slightly curved base and frayed tip. Labrum bilobed; width 1.5 times length; anterior surface with about 10 sensilla; ventral surface of each lobe with 1 isolated and a cluster of 2 or 3 sensilla; posterior surface spinulose, the spinules minute and in short arcuate rows. Mandible heavily sclerotized; pogonomyrmecoid but with only 1 medial tooth; medial border of base spinulose. Maxilla with apex conoidal; palp a skewed paxilla with 5 (4 apical and 1 lateral) sensilla; galea digitiform with 2 apical sensilla. Labium spinulose, the spinules minute and in short subtransverse rows; palp a slight elevation with 5 sensilla; opening of sericteries a small slit. Hypopharynx spinulose, the spinules minute and in short straight or arcuate subtransverse rows.

Immature larva. Length (through spiracles) about 1.8 mm. Similar to mature larva except as follows. Neck shorter and more slender. About 6 differentiated somites. Integument on venter of anterior somites with spinules in short transverse rows, sparse and isolated elsewhere. Body hairs of only type 1 and 0.012–0.05 mm long; 8 on AI, 6 on AII, 2 on AVII.

Material studied. 9 larvae from Sidi Amira, Forêt Maôra, Morocco, 14-V-1984, courtesy of X. Espadaler.



Figs. 1–10. 1 and 2. *Oxyopomyrmex* sp. 1. Mature larva. a, Head in anterior view, ×120; b, left mandible in anterior view, ×555; c, left mandible in lateral view, ×555; d, 2 body hairs, × 267; e, larva in side view, ×39. 2. Immature larva in side view, ×39. 3–6. *Rogeria scandens.* 3. Mature larva. a, Anchor-tipped hair, ×363; b, left maxilla in anterior view, ×168; c, left mandible in anterior view, ×168. 4. Immature larva. a, Anchor-tipped hair, ×363; b, left maxilla in anterior view, ×168; c, left mandible in anterior view, ×168. 5. Young larva. a, Anchor-tipped hair, ×363; b, left maxilla in anterior view, ×168; c, left mandible in anterior view, ×168. 6. Very young larva. a, Anchor-tipped hair, ×363; b, left maxilla in anterior view, ×168; c, left mandible in anterior view, ×168. 7. *Zacryptocerus laminatus christopherseni,* immature larva. a, Head in anterior view, ×41; b, left mandible in anterior view, ×128; c, anchor-tipped hair with "claws," ×339. 8. *Procryptocerus scabriusculus,* young larva. a, Left mandible in anterior view, ×145; b, head in anterior view, ×51. 9 and 10. *Orectognathus echinus.* 9. Very young larva. a, Larva in side view, ×21; b, 3 types of body hairs, ×133. 10. Young larva. a, Larva in side view, ×21; b, 3 types of body hairs, ×133.

Genus *Pheidole* Westwood
Pheidole bicarinata Mayr

D. E. Wheeler, 1982. Four larval instars may be distinguished by mandibles, hair pattern and spiracle sizes. SEM photographs of the 4 instars (p. 22), larval hairs (p. 27), sexual larvae (p. 32) and internal anatomy (p. 35).

TRIBE CREMATOGASTRINI
Genus *Crematogaster* Lund
Crematogaster scutellaris (Olivier)

Casevitz-Weulersse, 1983 and 1984. Three instars are described and illustrated by sketches and photographs, with special reference to the lateral expansions in some larvae. The instars are differentiated by size, pilosity and diameter of mesothoracic spiracles. The author's hypothesis: "these larvae are so abundantly fed that they acquire dilatations which may be compared to the special organs named 'exudatoria' by Wheeler (1918); these larvae may represent a 'stock' of future queens. The mechanism of formation of the dilatations as well as factors that influence the choice of the larvae that will be abundantly fed are as yet unknown" (1984:131).

TRIBE PHEIDOLOGETINI
Genus *Paedalgus* Forel
Paedalgus termitolestes Wheeler

Wheeler, 1918:301–302, figure 5. The text is essentially the same as the following; figure 43 is a repetition of figure 5

Wheeler, 1922:179–180, figure 43. The larvae are "white, nearly spherical, with short neck, small head, and very feebly developed mouth-parts, indicating that they are fed by the tiny workers with regurgitated liquid food. They are not 'glabres,' as Santschi described the larvae of *P. infimus,* but covered uniformly with short, stiff, sparse hairs, each of which has two recurved branches (Fig. 43*a* and *b*). Even in alcohol, the larvae cling compactly together in masses by means of these hooks. When stained and cleared, the larvae are seen to possess unusually voluminous salivary glands. The youngest individuals, scarcely 0.2 mm. long, have the receptacle full of a clear secretion (Fig. 43*a*). In older larvae (Fig. 43*b*), the secretion after dehydration forms great masses in the receptacles and lumen of the glands. As these organs are not used in spinning a cocoon, it is very probable that the secretion . . . is elaborated and used as a food for the workers (trophallaxis)."

TRIBE LEPTOTHORACINI
Genus *Leptothorax* Mayr
Leptothorax melas Espadaler et al.

Espadaler et al., 1984: "Big larvae are present in overwintering brood and develop usually as queens but can also grow into workers." Outlines of larvae.

Leptothorax obturator W. M. Wheeler

Wheeler, 1903:252. "The larvae are of a peculiar greenish tint."

Genus *Rogeria* Emery

Rogeria scandens (Mann)

Figs. 3–6

Mature larva. Length (through spiracles) about 2.8 mm. Profile pheidoloid. Similar to *R. procera* (1973:74) except as follows. Body hairs of 3 types: (1) about 0.04 mm long, simple; (2) 0.025–0.1 mm long, with bifid or multifid tip; (3) about 0.25 mm long, anchor-tipped, with sinuous shaft, 4–6 in a row across dorsum of each T2-AIII. Antennae at midlength of cranium. Head hairs 0.025–0.4 mm long, simple or with bifid tip. Labrum with anterior surface spinulose, the spinules coarse and isolated medioventrally, 6 isolated hairs about 0.013 mm long, and 4 isolated sensilla; each half of posterior surface with 4 isolated and a cluster of 3 sensilla. Mandible ectatommoid; heavily sclerotized; medial border of blade erose. Maxilla lobose; palp a short peg with 5 (3 apical and encapsulated, 1 lateral with a spine about 0.006 mm long and 1 basal with a hair about 0.013 mm long) sensilla.

Immature larva. Length (through spiracles) about 1.6 mm. Similar to mature larva except as follows. Body hairs shorter: (1) 0.025–0.05 mm long, few on venter of thorax; (2) 0.013–0.1 mm long, mostly bifid; (3) 0.2 mm long. Head hairs fewer; about 40. Mandible with apical and subapical teeth short.

Young larva. Length (through spiracles) about 1.2 mm. Similar to mature larva except as follows. Entire integument spinulose. Body hairs (1) 0.025–0.05 mm long, few, mostly on venter of thorax; (2) 0.025–0.075 mm long, long- to short-bifid; (3) about 0.2 mm long with a slightly curved shaft. Head hairs few (about 36). Labrum with fine spinules. Maxillary palp short and stout.

Very young larva. Length (through spiracles) about 0.87 mm. Similar to mature larva except as follows. Profile club-shaped. With minute spinules on venter of thorax. Body hairs (1) 0.006–0.03 mm long, on most somites; (2) 0.018–0.075 mm long, few; (3) about 0.125 mm long, with short nearly straight shaft. Head hairs 0.013–0.04 mm long, mostly simple, a few bifid-tipped. Labrum with a few minute spinules on anterior surface, hairs about 0.006 mm long. Mandible short and triangular; apex shorter; subapical teeth smaller; feebly sclerotized. Maxilla appearing adnate; palp a rounded knob with 5 sensilla; galea a slight elevation with 2 sensilla. Labium with palp represented by a cluster of 5 sensilla.

Material studied. 9 larvae from Barro Colorado Island, Panama, 19-IX-1983, courtesy of Diana E. Wheeler.

TRIBE TETRAMORIINI

Genus *Tetramorium* Mayr

Tetramorium caespitum (Linnaeus)

Hinton, 1951:156. The larva of *Maculinea alcon* F. [Lepidoptera: Lycaenidae] prey upon the larvae, sucking out the juices.

Poldi, 1967: The author reared workers from eggs using as food only nutritive eggs. Figure 1 on p. 325 is an outline of a larva in profile.

TRIBE CEPHALOTINI

Genus *Procryptocerus* Emery

Procryptocerus scabriculus Emery

Fig. 8

Mature larva (?). Length (through spiracles) about 4 mm. Similar to *P. adlerzi* (1973:79) except as follows. Head on anterior end. Body hairs of 4 types: (1) 0.003–0.13 mm long, longest on posterior surface of AX; (2) 0.025–0.1 mm long, with straight shaft and frayed tip, most numerous on T1; (3) about 0.2 mm long, anchor tipped, 4 in a row across dorsum of each AI-AIV; (4) about 0.05 mm long, with slender flexuous tip, few, on venter of T1. Integument on venter of T1 and T2 with few minute spinules. Cranium transversely subelliptical. Head hairs numerous (about 100). Of 2 types: (1) 0.025–0.05 mm long, with long flexuous tip; (2) 0.038–0.063 mm long, with frayed tip, longest on lower margin of clypeus. Labrum trapezoidal; anterior surface with a row of 6 hairs 0.019–0.03 mm long, simple, slightly curved, 10 sensilla on and near ventral border; posterior surface with 6 isolated and a cluster of 3 sensilla.

Immature larva. Length (through spiracles) about 2.5 mm. Similar to mature larva except as follows. Body hairs of only 3 types: (1) similar to mature larva; (2) 0.012–0.1 mm long; (3) about 0.175 mm long; (4) lacking. Head hairs numerous (about 75); (1) shorter (0.006–0.024 mm long). Labial palp a slight knob with 5 sensilla.

Young larva. Length (through spiracles) about 1.7 mm. Similar to immature larva except as follows. Body nearly same diameter throughout. Head on anterior end. Body hairs few. Of 3 types: (1) 0.013–0.08 mm long, on dorsal and lateral surfaces, with bifid to multifid tip; (2) 0.006 mm long, simple, on all surfaces; (3) about 0.11 mm long, anchor-tipped, 4 on dorsum of each AI-AVI, 2 on AVII. Head hairs few (about 20); of only 1 type: 0.013–0.038 mm long, with frayed tip. Mandible more slender and with larger teeth. Maxilla appearing adnate, lobose; palp an irregular knob with 5 sensilla; galea a slight elevation with 2 sensilla. Labial palp an irregular knob with 5 sensilla.

Material studied. 8 larvae from Costa Rica, 25-VIII-1983, courtesy of Diana E. Wheeler.

Genus *Zacryptocerus* Ashmead

Zacryptocerus laminatus christopherseni (Forel)

Fig. 7

Immature larva. Length (through spiracles) about 5 mm. Similar on *Z. minutus* (called *Paracryptocerus minutus* 1954:155). Head on anterior end; body club-shaped. Leg vestiges prominent; gonopod vestiges of AIX distinct; wing vestiges distinct. Integument densely spinulose, the spinules minute and in short to long subtransverse rows. Body hairs: (1) 0.01–0.075 mm long, simple, most numerous on T1, on all surfaces of T1 and T2 and venter of T3, AI and AII, decreasing in number posteriorly; (2) about 0.225 mm long, anchor-tipped (some with "claws"), 4–6 in a transverse row across dorsum of each T3 and AI-AV. An integumentary structure (ridges and/or grooves?) dorsolateral to each antenna. Antennae just below midlength of cranium. Head hairs numerous (about 50), short (0.025–0.075 mm long), simple. Ventral border of labrum feebly 4-lobed; posterior surface with sparse transverse rows of spinules. Maxilla appearing adnate; palp a low irregular knob with 5 sensilla; galea a small knob with 2 sensilla. Labium with a few transverse rows of minute spinules; palp a slight elevation with 5 sensilla.

Material studied. 2 larvae from Panama, 2-III-1983, courtesy of Diana E. Wheeler.

TRIBE BASICEROTINI

Genus *Octostruma* Forel

Octostruma inca Brown and Kempf

Correction. Wheeler and Wheeler, 1977:600–601. Change the mandible shape to pogonomyrmecoid.

TRIBE DACETINI

Genus *Orectognathus* F. Smith

Orectognathus echinus Taylor and Lowery

Figs. 9, 10

Mature larva. Length (through spiracles) about 5 mm. Similar to *O. clarki* (1954: 126) except in the following details. Body hairs (1) 0.1–0.35 mm long; (2) 0.065–0.3 mm long, with few to many denticles of various lengths, on all somites; (3) about 0.375 mm long, 4 in a row across dorsum of each AII-AV or -AVI. Antenna with 3 or 4 sensilla each with a prominent spinule. Head hairs longer (0.05–0.2 mm long). Labrum with 3 hairs about 0.012 mm long; spinules on posterior surface fewer and longer. Mandible with base roughened with transverse ridges. Maxillary palp digitiform with 5 (2 apical, 2 subapical and 1 lateral) sensilla.

Immature larva. Length (through spiracles) about 3.4 mm. Similar to mature larva except as follows. Abdomen more swollen. Anus with anterior and posterior lips. Clypeus with subtransverse rows of minute spinules. Each half of labrum with anterior surface bearing 3 or 4 hairs about 0.09 mm long; ventral surface with 1 isolated and 2 contiguous sensilla; posterior surface spinulose, the spinules minute and in short to long transverse rows. Labium transversely subelliptical.

Young larva. Length (through spiracles) about 2.9 mm. Similar to immature larva except as follows. Neck more slender. Body hairs: (1) 0.075–0.175 mm long; (2) 0.075–0.4 mm long; (3) 0.225–0.4 mm long. Antennae at midlength of cranium.

Very young larva. Length (through spiracles) about 1.6 mm. Body short, stout, thorax curved ventrally. Diameter of T2 spiracle 0.013 mm, remainder decreasing slightly posteriorly. Integument of AX with minute spinules in short transverse rows. Body hairs: (1) 0.018–0.15 mm long, slightly curved, smooth or with minute denticles, mostly on ventral surface; (2) about 0.05 mm long, slightly to deeply bifid, some with denticles, on lateral and dorsal surfaces; (3) about 0.2 mm long, anchor-tipped [hairs broken] at least on T3-AVI. Antenna a small knob with 3 sensilla each with a long spinule. Head hairs 0.08–0.18 mm long, simple. Mandible feebly sclerotized, with 1 apical and 2 short medial teeth. Galea a short cone with 2 apical sensilla.

Material studied. 6 larvae from Mt. Missimi, 1,550 m, Papua New Guinea; 30-V-1980, coll. Y. D. Lubin, courtesy of R. R. Snelling.

Orectognathus versicolor Donisthorpe

Carlin, 1981:223. Small photograph of larvae.

Hölldobler, 1981:246. Small photographs of larvae and (p. 248) of worker carrying larva.

TRIBE ATTINI

Genus *Acromyrmex* Mayr

When we were preparing our first publication on Attini (1948) our *Acromyrmex* material consisted of three larvae of *A. lundi* and three of *A. octospinosus.* Presumably the latter were not in good condition for we did not draw a whole larva; furthermore the heads of these two species are generically different. So for 40 years we have had doubts about this genus. Dr. Febvay's generous contribution has stilled our doubts about *A. octospinosus.* Can anyone do as much for *A. lundi*?

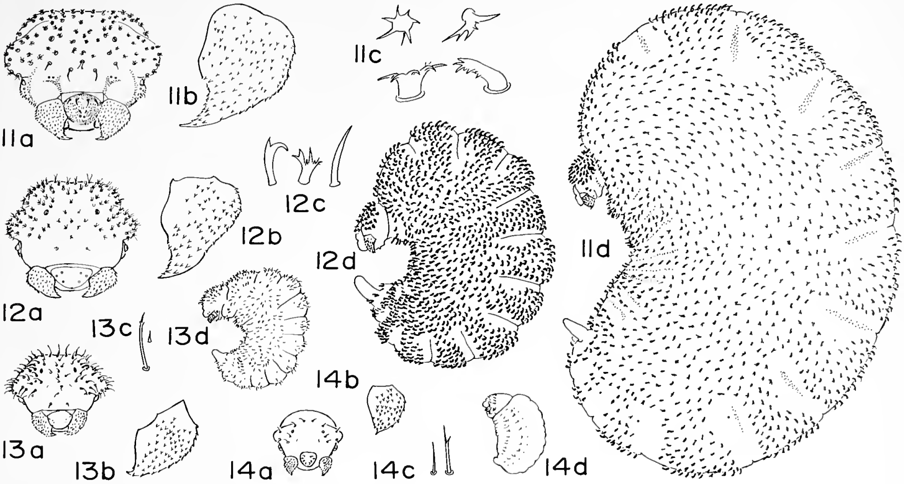
Acromyrmex octospinosus (Reich)

Figs. 11–14

Mature worker larva. Length (through spiracles) 6.5–8.8 mm. Body attoid. Head on ventral surface at a considerable distance from anterior end. Anus ventral and with a digitiform posterior lip. Segmentation indistinct. Leg, wing and gonopod vestiges present. Diameter of T2 spiracle 0.025 mm, remaining spiracles decreasing slightly posteriorly. Intersegmental structures dorsolateral and ventrolateral on thorax and AI-AVI. Integument on all surfaces of posterior somites and venter of anterior somites with minute spinules in transverse rows. Body hairs inconspicuous, moderately numerous, very short (0.025–0.06 mm long), very stout, bent posteriorly, apical margin frayed. Cranium transversely subelliptical, with bulging genae. Antenna a small pit with 3 sensilla at the bottom; at upper fourth of cranium. Head hairs abundant (about 120), but lacking on lower fourth; similar to body hairs. Labrum transversely subelliptical; anterior surface with 4 simple hairs; entire anterior surface with rather coarse isolated spinules and about 7 sensilla each with a minute spinule; ventral border with isolated spinules; posterior surface spinulose, the spinules in short to long transverse rows. Mandible attoid; apical tooth moderately sclerotized; no medial teeth; all surfaces with numerous large sharp-pointed denticles. Maxilla very long and narrow, apex round-pointed; integument sparsely spinulose; palp a skewed sclerotized frustum with 2 apical and 1 basal sensilla; galea a sclerotized peg with 2 apical sensilla. Labium spinulose, the spinules minute and in numerous arcuate rows; palp a low knob with 5 sensilla; opening of sericteries a transverse slit in a depression. Hypopharynx spinulose, the spinules in rather long subtransverse rows.

Immature larva. Length (through spiracles) 4–4.4 mm. Similar to mature larva except as follows. Segmentation distinct. Diameter of T2 spiracle 0.016 mm. Head hairs slightly less numerous (about 110). Apical tooth of mandible not much larger than denticles. Spinules of hypopharynx in short to long subtransverse rows.

Young larva. Length (through spiracles) 2–2.8 mm. Similar to immature larva except as follows. Profile crescentic; diameter greatest at T3. Anus ventral, with posterior lip forming a short tail. Diameter of T2 spiracle 0.009 mm, remaining



Figs. 11–14. *Acromyrmex octospinosus.* 11. Mature larva. a, Head in anterior view, ×44; b, left mandible in anterior view, ×119; c, body hairs in surface view (top) and side view (bottom), ×169; d, larva in side view, ×20. 12. Immature larva. a, Head in anterior view, ×44; b, left mandible in anterior view, ×119; c, body hairs, ×169; d, larva in side view, ×20. 13. Young larva. a, Head in anterior view, ×44; b, left mandible in anterior view, ×119; c, body hairs, ×169; d, larva in side view, ×20. 14. Very young larva. a, Head in anterior view, ×44; b, left mandible in anterior view, ×119; c, body hairs, ×169; d, larva in side view, ×20.

spiracles decreasing slightly posteriorly. Integument with minute spinules which are isolated or in short rows on all surfaces of AVIII-AX, venter of anterior somites and dorsal surface of abdominal somites. Body hairs moderately numerous, but absent in vicinity of spiracles; of 1 type: 0.006–0.05 mm long, with stout base and multifid tip. Head hairs moderately numerous (about 66), short (0.013–0.05 mm long), ranging from slender to stout, with multifid tip. Labrum with anterior and ventral surfaces sparsely spinulose, the spinules small and sharp-pointed; posterior surface spinulose, the spinules small and isolated ventrally, minute and in short rows dorsally; anterior surface with 6 sensilla; ventral surface with 4 sensilla. Mandible attoid, but with apical portion shorter and denticles with sharper tips. Maxillary palp a sclerotized knob with 4 (3 with a spinule each) apical sensilla; galea a very low feebly sclerotized knob with 2 apical sensilla. Labium with spinules in rows of 4–6; palp a small knob with 5 sensilla; an isolated sensillum between each palp and the opening of the sericteries. Hypopharynx densely spinulose, the spinules minute and in short rows.

Very young larva. Length (through spiracles) about 0.9 mm. Similar to young larva except as follows. Short, plump and slightly curved ventrally; diameter greatest at AIII and AIV. Head on anterior end. Anus with prominent lips, the posterior forming a conspicuous knob. Spiracle of T2 0.003 in diameter, remaining spiracles decreasing in diameter posteriorly. Somites feebly differentiated. Integument spinulose, the spinules rather large and isolated, except a few larger and in short rows on venter of thorax. Body hairs few and short, all ventral to spiracles, none on AIX and AX. Of

2 types: (1) short (0.006–0.038 mm long), simple; (2) 0.013–0.038 mm long, with bifid (rarely multifid) tip. Antennae minute, with 3 sensilla, at upper third of cranium. Head hairs few (about 12) and lacking on lower fourth of cranium. Of 2 types: (1) 0.006–0.025 mm, simple; (2) about 0.025 mm long, with multifid tip. Labrum with all surfaces bearing rather coarse isolated spinules; anterior surface with 6 sensilla, each with a spinule. Mandible feebly sclerotized, attoid but with apical portion shorter than in mature larva. Maxillary palp an irregular knob with 2 small sensilla each bearing a spinule and 1 large and encapsulated; galea an irregular swelling with 2 sensilla. Labium subhemispherical, with numerous short transverse rows of 2 or 3 minute spinules; palp represented by 2 minute sensilla.

Sexual larva. Length (through spiracles) 8.9–10 mm. Similar to mature worker larva.

Material studied. Numerous larvae from Guadeloupe, French West Indies, courtesy of G. Febvay.

Torre-Grossa et al., 1982: Four instars distinguishable by length of hairs and by diameter of peritreme of mesothoracic spiracle. Sexual larvae have a fifth instar.

Febvay and Kermarrec, 1981: "Les adultes dépendent, comme d'autres Hyménoptères . . . des sécrétions larvaires pour la fourniture d'un supplément en acides amines" (p. 312). "The larval midgut shows a biologically important endopeptidasic activity (chymotrypsin)" (p. 314).

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Received September 23, 1985; accepted March 14, 1986.

J. New York Entomol. Soc. 94(4):500–511, 1986

SEEVERSIELLA BISPINOSA, A NEW GENUS AND SPECIES OF ATHETINE ALEOCHARINAE (COLEOPTERA: STAPHYLINIDAE) FROM NORTH AMERICA

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Abstract.—Seeversiella bispinosa, a new genus and species of athetine aleocharine staphylinid, is described and illustrations of structural features are provided. Members of *Seeversiella* are particularly distinctive among known North American aleocharines because of the presence of a large spine on each apico-lateral margin of abdominal tergum III and a medial carina on tergum VII of most males. The species was first noted as representing a "new genus" in a key to genera of North American Aleocharinae provided in 1978 by Dr. Charles Seevers, but he did not give it a formal name or provide a description. Modification of pertinent couplets of Seevers' key is provided which allows for identification of specimens of *Seeversiella.*

The staphylinid subfamily Aleocharinae represents one of the most taxonomically difficult large sections of the Coleoptera in North America (Arnett, 1968) in spite of their abundance and great diversity in many microhabitats. At present, it is virtually impossible to confidently assign many specimens to one of the 200 or so genera described for America north of Mexico without comparisons with type material or a major reference collection. With this perspective in mind, I would normally consider it premature to describe new North American genera in the Aleocharinae, except possibly in those few tribes or subtribes which have received modern revisionary studies. Until the numerous genus level groups already in the literature are properly delimited, described and illustrated and functional keys are provided for their separation, it seems that description of new taxa is only likely to add more confusion to an already difficult subfamily. However, the genus described in this paper is recognized to be undescribed as a result of a rather unusual set of circumstances, and, for reasons outlined below, I feel that it is timely to provide a name with adequate description and illustrations.

The unusual circumstances surrounding this new genus began with the studies of Dr. Charles Seevers on the systematics of the higher taxa of North American Aleocharinae. These studies, which represent the only serious and comprehensive attempt to bring some degree of order out of the chaos of numerous, superficially described genera for North American aleocharines, were undertaken primarily at the Field Museum of Natural History in Chicago, where Dr. Seevers was a research associate. Unfortunately, at Dr. Seevers' death in 1965, his studies had not been completed. However, he had amassed a considerable quantity of manuscript copy in advanced stages of completion toward a revision of genera of the Aleocharinae. Recognizing the importance and irreplaceable value of the information included in Seevers' unpublished manuscript, Dr. Henry Dybas, Curator of Insects, and Dr. Rupert Wenzel, Chairman of the Department of Zoology, both of the Field Museum, elected to edit, organize and ultimately publish this manuscript in spite of its incompleteness.

They employed Dr. Lee H. Herman, a noted specialist on the Staphylinidae, to edit and check the accuracy of the manuscript and to provide annotations as appropriate. However, major revision and completion of the manuscript was not attempted, and it was published in 1978 as nearly as possible in the form left by Dr. Seevers. It is clearly incomplete, uneven in its treatment and erroneous in many areas, all of which would not have been true had Dr. Seevers been able to complete his work. Yet, because it provides the only comprehensive basis for addressing problems associated with North American aleocharines, this revision has become the standard reference for study of this group.

In Seevers' revision, the first half of couplet 69 of the key to genera (page 46) provides for identification of a "new genus." No formal name is provided and no other mention of this "new genus" occurs elsewhere in the text. In an annotation, Dr. Herman notes that he was unable to find any reference to it in the text or catalogue that he edited. Considerable searching in the collection of the Field Museum has failed to turn up any specimens which are clearly labeled as material that Seevers had intended to use for description of this new genus. However, very distinctive specimens which generally agree with the key provided were found amongst the alcohol preserved collections. This material clearly represents an undescribed genus and is characterized by the highly distinctive male secondary sexual features used in Seevers' key. There can be little doubt that this material represents the new genus that Seevers had planned to key out in this couplet, even if not the material he actually examined. Since this time, additional material has been found, some in the collection of the American Museum of Natural History, and some as a result of my own collecting and that of others. The most notable collections were made by Dr. Milton Sanderson who has collected long series of members of this genus on a number of occasions and has kindly made them available for my study.

In order to clarify this part of Seevers' (1978) revision, it seems very pertinent and timely to provide a formal name and description for this new genus.

Seeversiella, new genus

Diagnosis. Members of *Seeversiella* can be easily distinguished from other Aleocharinae by the combination of: quadrate to slightly elongate head; eye length less than 0.5 times length of head and shorter than distance from posterior margin of eye to base of head (Fig. 1); more or less quadrate pronotum (Fig. 2); head and pronotal setal patterns with setae directed medially (Figs. 1, 2); elytra with sinuate or posterolaterally directed setal pattern (Fig. 3); hypomera fully visible in lateral aspect; mesosternum without medial carina (Fig. 4); known species with mesosternal process: isthmus: metasternal process in ratio of 26:22:7 (Fig. 4) (see Seevers, 1978, p. 27); tarsal formula 4,5,5; abdominal terga III–IV or III–V moderately to slightly impressed basally; male abdominal tergum III with slight to marked lateral spinose processes (Fig. 10), and tergum VII with medial carina; female without secondary sexual modifications; aedeagus with internal hooks and spinose areas (Fig. 11); and spermatheca simple (Fig. 3).

Description. Moderate sized, length of known species approximately 3.1–4.0 mm. Body shape elongate, slender, more or less flattened. Body color of known species uniformly dark reddish brown to dark brown. Body sculpture reticulate throughout with microsculpture denser and more prominent on head, pronotum and elytra, integument surface dull to slightly shining; integument moderately and very finely pubescent, microsetae appressed; macrosetae present, inconspicuous; punctures moderately dense, very fine.

Head (Fig. 1) quadrate to slightly elongate in dorsal aspect, 1.0–1.1 times as long as wide, basal angles broadly rounded, neck absent. Eye size small, 0.30–0.40 times length of head. Tempora long, 1.5–1.8 times length of eye, broadly rounded basally. Dorsal pubescence directed medially. Infraorbital carina slight basally, fading and absent anteriorly and ventrally. Antenna (Fig. 9) moderately short, about as long, or slightly longer than, head and pronotum together in most; very slightly incrassate; article 4 more or less quadrate to very slightly transverse, articles 5–10 slightly to moderately transverse and increasing in width to more apical articles.

Labrum as in Figure 5. Right mandible with small internal tooth, left mandible without internal tooth; mandibular apices acute, entire; molar region slightly developed, without dense patch of denticles but with single row of spinose teeth on inner edge; prostheca with spinose teeth medially (Fig. 6). Maxilla (Fig. 8) with galea slightly longer than lacinia; galea densely pubescent in apical 0.3 with long filiform setae; lacinia with comb of single row of large teeth apico-medially and dense patch of recurved setae dorso-medially; maxillary palpus 4 articled, without accessory pseudosegment on article 4. Labium (Fig. 7) with palpi 3 articled, not styliform; ligula short, about 1.0–1.1 times as long as width of base, deeply divided to near base into 2 bluntly rounded, divergent lobes; medial setae 2, widely separated at base, distance between setal insertions greater than width of ligula; prementum with several pseudopores medially and posterior to medial setae, and several large pores and 1 spinose pore laterally on each side.

Pronotum (Fig. 2) more or less quadrate, about 1.0 times as wide as long; slightly convex in cross section; anterolateral margins obtusely rounded and slightly depressed, sides more or less straight; posterior angles rounded, not bisinuate basally; pronotal edge margined with a fine raised bead; pubescence with setae directed medially. Hypomera broadly visible in lateral aspect. Elytra (Fig. 3) slightly longer than pronotum (1.15–1.20 times longer); outer apical angles evenly rounded, not sinuate; pubescence arranged in a sinuate pattern or directed more or less posteriorly. Mesosternum not carinate medially; mesosternal process pointed, acute, reaching to approximately middle of coxal cavities; metasternal process short, broadly rounded; isthmus long; coxal cavities contiguous posteriorly, coxae very narrowly separated. Mesosternal process : isthmus : metasternal process ratio of known species 26:22:7. Metepisternal setae numerous, in 2–3 irregular rows, setose area not delimited by a carina. Legs with tarsal formula 4,5,5; hind tarsomere 1 approximately 1.2–1.3 times as long as 2.

Abdomen with general shape elongate, more or less parallel sided or broadly and slightly tapered from basal segments to acute apex. Terga III–IV or III–V moderately to slightly transversely impressed basally. Sterna not impressed. Tergum X triangular, narrow basally; setae absent postero-medially to produce a moderately narrow inverted V-shaped setal patch.

Aedeagus (Fig. 11): Median lobe with numerous internal sclerotized hooks and setose areas.

Spermatheca (Fig. 13): Simple, basal bulb small, neck not elongate or coiled.

Secondary sexual characteristics: Male with lateral margins of tergum III prolonged into very slight to very markedly developed spinose processes (Fig. 10) and tergum VII with prominent to very slight medial carina extended from anterior 0.2 to posterior margin, or only on posterior 0.5, or absent (in some). Female unmodified.

Type species. Seeversiella bispinosa, new species, here designated.

Distribution. Presently known only from the range of the type species.

Etymology. The genus name "Seeversiella" is chosen to honor Dr. Charles Seevers, who first recognized that this taxon represented an undescribed genus, and in recognition of his considerable contributions to knowledge of the North American Aleocharinae.

Discussion. Among Aleocharinae from America north of Mexico the genus *Seeversiella* is quite distinctive and can be recognized by those characteristics given in the diagnosis. Most notable among these are the striking secondary sexual characteristics of male specimens. Similar structures have not been described for any other group of North American aleocharines. However, some care should be used in basing identifications solely on these secondary sexual features.

I have seen specimens of an apparently undescribed genus of aleocharine from Mexico (Veracruz and Tamaulipas) which have male secondary characteristics amazingly similar to those of *Seeversiella* as well as having general habitus and color features which are also similar. Most remarkable are the large lateral spines on the apical margin of abdominal tergum III (some have the medial area of this tergum also produced posteriorly as a triangular spine) and a carinate knob or spine medially on tergum VII. These are so superficially similar that initial examination suggested that they may represent another species in the same genus. However, upon closer examination, the marked differences between the Mexican and United States specimens became apparent. They differ in a number of characteristics which have previously been used to describe taxa at the generic, or higher, level, but most notably in the pair of coeloconic sensory structures of antennomere 11 and the 5,5,5 tarsal formula of the Mexican specimens.

Clearly the Mexican specimens are in the Oxypodini, in contrast to the athetine relationships of *Seeversiella.* The remarkable overall resemblance, and especially the striking similarity in secondary sexual characteristics, represents an instance of considerable parallelism in the Aleocharinae. It also graphically illustrates that secondary sexual characteristics alone are not adequate for correctly identifying a specimen as *Seeversiella.*

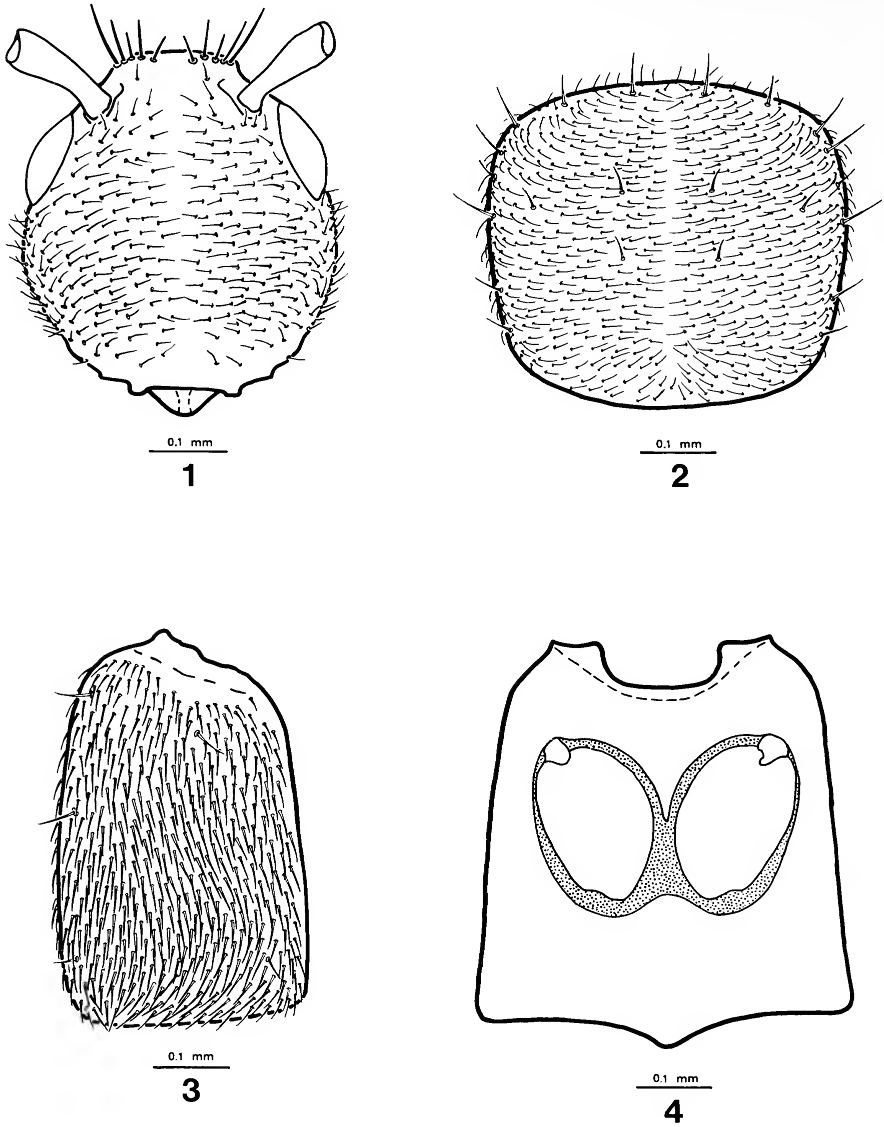
Presently, only a single species is included in *Seeversiella.* This suggests that when other species are discovered, the generic description provided here may be shown to be incorrect in some details and will consequently require modification. However, characteristics used in the generic description are those which have previously proven to be useful in descriptions of athetine aleocharines, and, therefore, I expect any required modifications to be minimal.

Seeversiella bispinosa, new species

Figs. 1–13

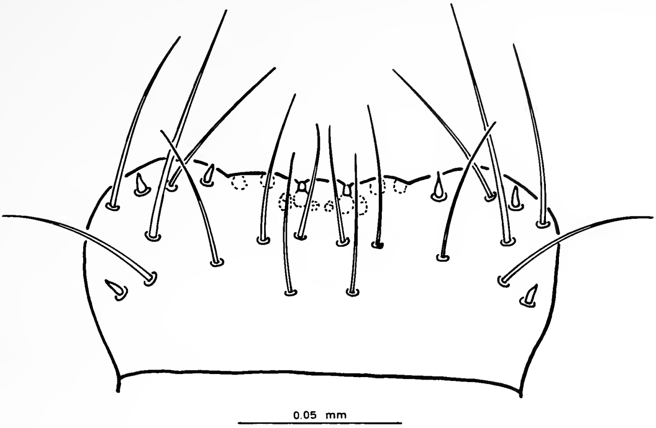
Description. Length 3.1–4.0 mm. Body color uniformly dark reddish brown to dark brown.

Head (Fig. 1) markedly reticulate with dense, well defined irregularly isodiametric sculpticells, surface very slightly shining; microsetae short, moderately dense, ap-



Figs. 1–4. *Seeversiella bispinosa,* new species. 1. Head, dorsal aspect. 2. Pronotum. 3. Left elytron. 4. Meso-metasterna and mesocoxal cavities.

pressed; punctures very fine, inconspicuous. Antenna (Fig. 9) with articles 1–3 elongate, more or less equal in length; article 4 quadrate (in most) to very slightly transverse; article 5 transverse, approximately 1.1–1.2 times as wide as long; articles 5–10 decreasing in length and becoming more transverse to anterior articles; article 10 transverse, approximately 1.6–1.7 times as wide as long; article 11 about as long as



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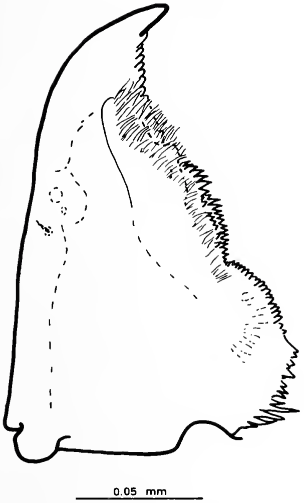

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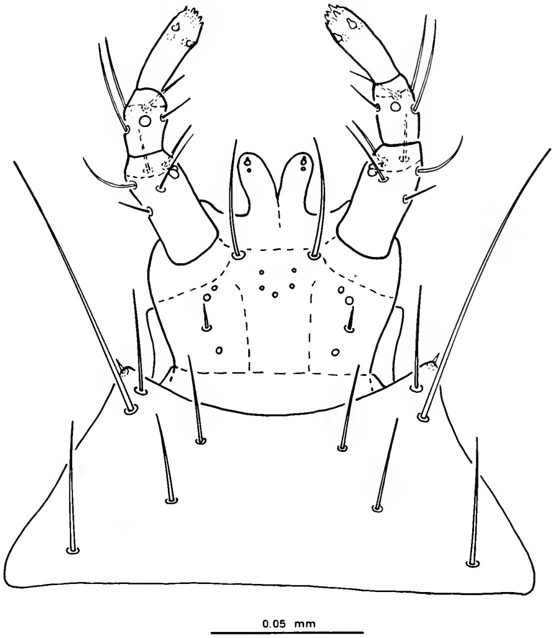

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Figs. 5–7. *Seeversiella bispinosa,* new species. 5. Labrum. 6. Mandible. 7. Labium, ventral aspect.

9 and 10 together. Pronotum (Fig. 2) densely reticulate with irregularly isodiametric sculpticells, surface very slightly shining; pubescence with setae directed medially, setae moderately dense, short, appressed; punctures very fine, inconspicuous. Elytra (Fig. 3) slightly wider at base than maximum width of pronotum; sculpture densely isodiametrically reticulate, integument more or less dull to very slightly shining; setation moderately dense, short, appressed, in sinuate pattern (in most) or directed more or less posteriorly in some; punctures very finely and slightly asperite. Abdominal terga with moderately sparse pubescence, microsetae fine, short and appressed; punctures very fine; microsculpture present, reticulate, distinct but less dense and well defined than on anterior parts of body, integument shining. Abdominal sterna with moderate pubescence, microsetae very fine, short, appressed; sculpture reticulate, integument shining.

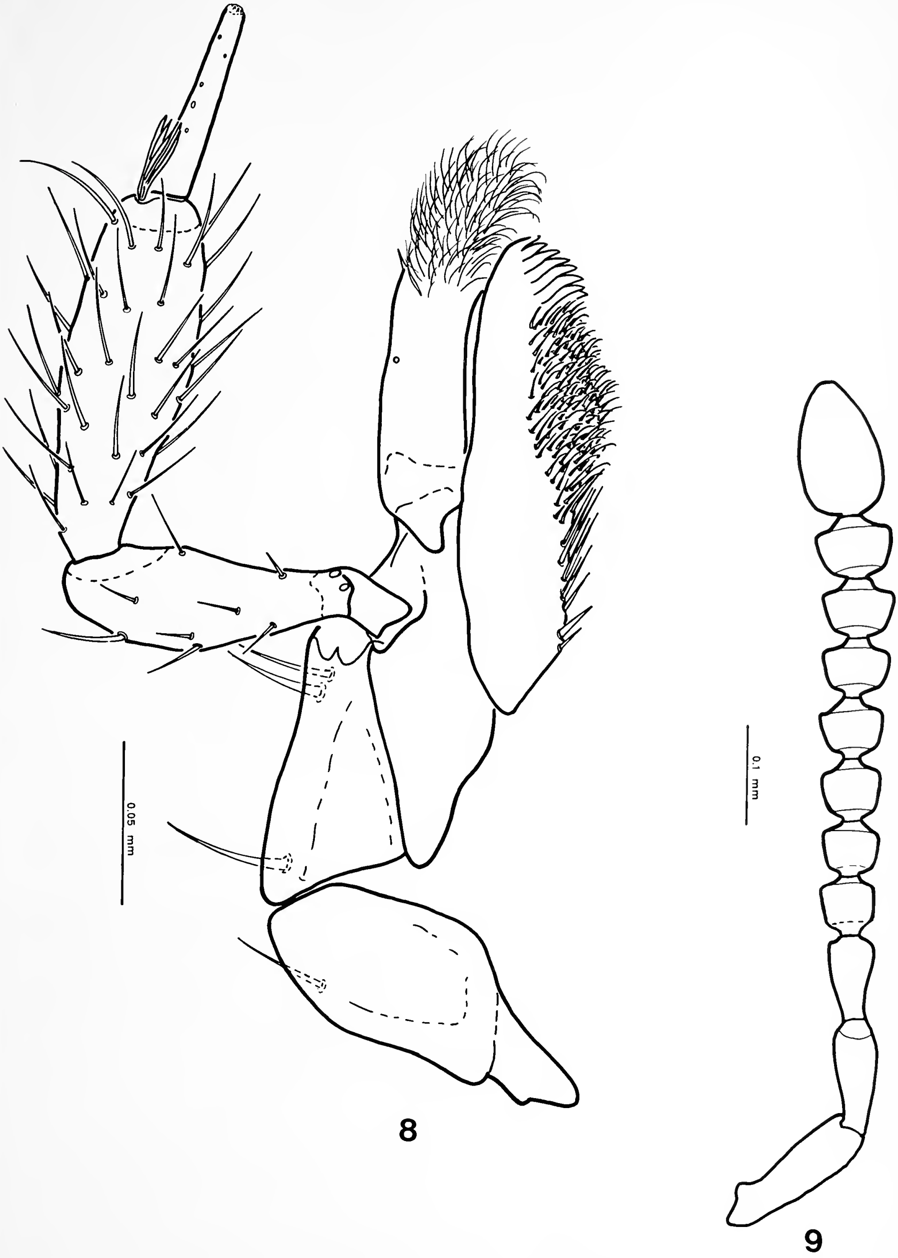
Secondary sexual characteristics: Male with characteristics of the genus; lateral margins of tergum III produced as spinose processes and tergum VII with longitudinal medial carina extended from anterior 0.2 to apex of tergum or limited to posterior 0.5 of tergum; development very various among males, some with lateral spines of tergum III inconspicuously produced (Fig. 10A), or, in a very few, absent, and medial carina of tergum VII absent to lateral spines and medial carina extremely large and prominent (Fig. 10C). Female unmodified.

Aedeagus: Median lobe (Fig. 11) with large oval depressor plate and small apical process; internal sclerites with pair of large, well sclerotized hooks postero-ventrally and sclerotized flagellar process, and numerous setose internal membranes. Parameres (Fig. 12) with apical lobe of paramerite small, most basal apical process seta at least 2.0 times longer than other 3 setae.

Spermatheca (Fig. 13): Simple; basal bulb small; neck constricted and apex inflated.

Type. Holotype, male, and allotype, female, each with labels as follows: Arizona: San Francisco Mtns., Hart Prairie rd. (418), 11-IX-1982, M. W. Sanderson, woody debris base dead ponderosa pine; Holotype (on female, Allotype), *Seeversiella bispinosa,* n. sp., Designated J. S. Ashe, 1985. Both holotype and allotype are deposited in the collection of the Field Museum of Natural History, Chicago, Illinois.

Paratypes. 168. Distributed in the following museums: Field Museum of Natural History, Chicago, Illinois (FMNH); American Museum of Natural History, New York, New York (AMNH); United States National Museum, Washington, D.C. (USNM); and, Canadian National Collection, Ottawa, Ontario (CNC). ARIZONA: Coconino Co., Hutch Mtn., rd. 124H, 14-X-1984, M. W. Sanderson, douglas fir duff, some aspen, 8 males, 9 females (FMNH); same locality, 8-X-1985, M. W. Sanderson, oak-pine-fir debris, 5 males, 7 females (FMNH); San Francisco Mtns., Hart Prairie rd. (418), 11-IX-1982, M. W. Sanderson, woody debris base dead ponderosa pine, 34 males, 34 females (3 males, 1 female on microslides) (FMNH, USNM, CNC); same locality, 24-V-1983, M. W. Sanderson, debris at base of ponderosa pine, 9 males, 11 females (FMNH); San Francisco Mtns., Fairfield Snowbowl, rd. 516, 14-XI-1984, M. W. Sanderson, aspen-fir duff, 2 males, 1 female (FMNH); San Francisco Mtns., Lockett Meadow, 19-IX-1981, berlese sample under aspens, 4 males (FMNH); same locality, 12-X-1984, M. W. Sanderson, aspen duff, 2 males, 2 females (FMNH); Sawmill Springs, 6 mi E FH3, rd. 124H, 18-XI-1984, M. W. Sanderson, mostly ponderosa pine duff, 2 males, 1 female (FMNH); West Fork Oak Creek Canyon, 1-XI-1984, M. W. Sanderson, leafy-woody debris on hillside, 1 male (FMNH); Gra-



Figs. 8, 9. *Seeversiella bispinosa,* new species. 8. Maxilla, dorsal aspect. 9. Right antenna.

ham Co., Pinalino Mtns., mi post 127, 6,500 ft, 16-V-1968, L. Herman, leaf litter, 2 males, 6 females (AMNH); Pima Co., Santa Catalina Mtns., elev. 8,000 ft, 16-VI-1968, 7 males, 1 female (AMNH); Santa Catalina Mtns., Bear Wallow, 12–17-VII-1916, 1 male (AMNH); Santa Catalina Mtns., Mt. Lemmon Ski Area, 8,500 ft, 24-VII-1983, J. S. Ashe, ex. *Fomitopsis pinicola,* 1 male (FMNH); same data, ex. *Pleurotus* sp., 1 male (FMNH); same data, ex. *Hirchioporus abietinus,* 1 male, 1 female (on microslides) (FMNH). COLORADO: Dolores Co., 19 mi NE Dolores (Montezuma Co.), W. Dolores River, 7,600 ft, 22-VII-1976, L. and N. Herman, 1 male (AMNH). MICHIGAN: Gogebie Co., Ottawa Natl. For., Sylvania Tract, 13-VIII-1977, J. Wagner, floor litter and mycelium, 5 males, 8 females (2 males, 1 female on microslides) (FMNH). NEW MEXICO: Bernalillo Co., Sandia Mtns., 9,300 ft, 21-VIII-1975, S. Peck, oak-pine-douglas fir litter, 1 male (FMNH); Grant Co., Mimbres Mtns., 20.8 mi W Hillsboro, hwy 90, 31-VII-1983, J. S. Ashe, ex. gilled mushroom, 1 male (FMNH).

Distribution (Fig. 14). *Seeversiella bispinosa* is known from the montane regions of the Southwestern United States, including the Pinalino, Santa Catalina, and San Francisco Mountains of Arizona, the Mimbres and Sandia Mountains of New Mexico and the southern Rocky Mountains in Colorado. It is also known from a disjunct population in the Upper Peninsula of Michigan. This distribution suggests that subsequent collecting may show this species to be much more widespread in the montane areas of the Rocky Mountain States and the Southwest, and perhaps also in upland regions of the southern portions of the boreal forest.

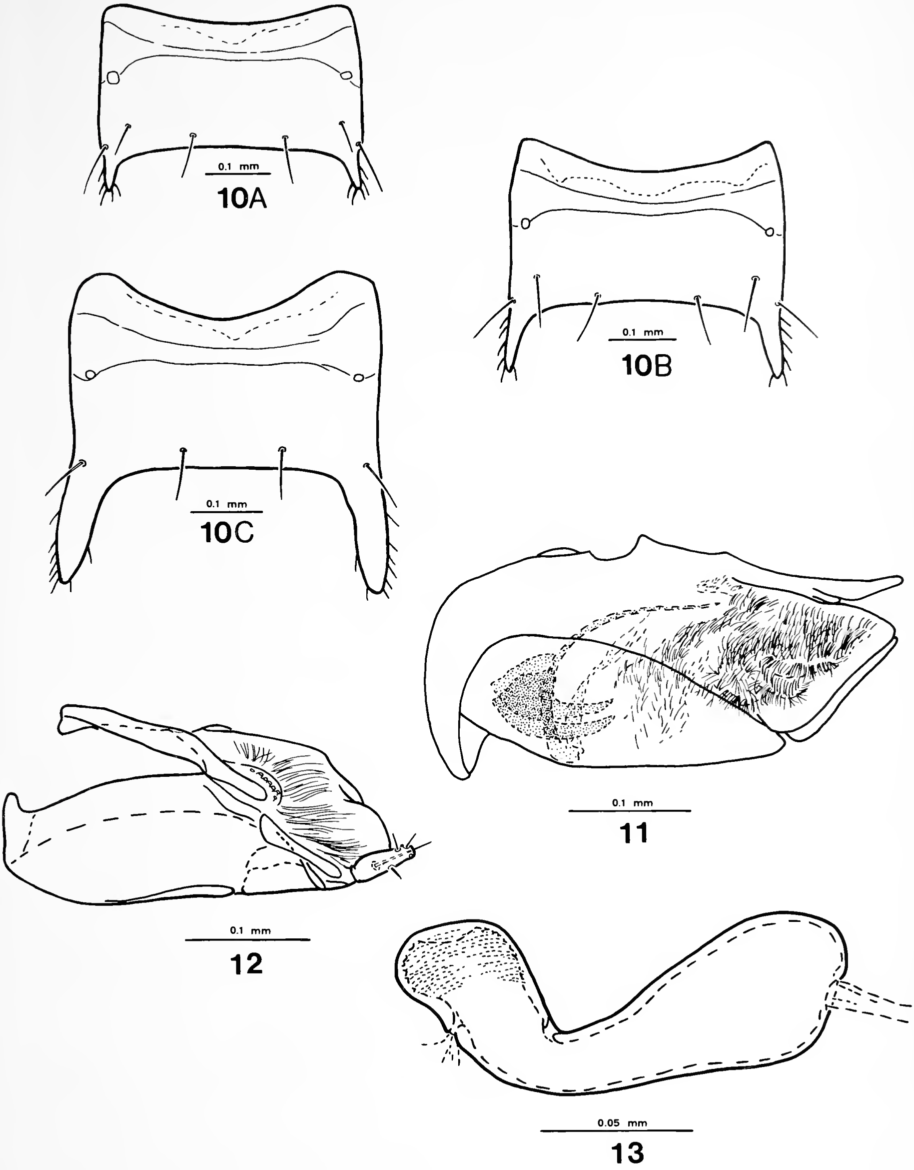
Habitat. Members of *Seeversiella bispinosa* have been most frequently collected in association with mixed conifer and aspen litter or forest duff. The largest collections have been from woody debris at the base of ponderosa pines. Specimens from Michigan were collected from "litter and mycelium." The type of litter cannot be deduced from the specimen labels; however, the primary forest type of the Upper Peninsula of Michigan is mixed conifer and aspen. It seems likely that these specimens were collected from litter of this type. A few specimens have been collected from mushrooms. However, they are not abundant in this habitat, and their association with fungal fruiting bodies is probably incidental or in association with litter which often accumulates around more persistent mushrooms.

Specimens of *S. bispinosa* have been collected in all months from May through November.

Etymology. The species name "bispinosa" is chosen to refer to the two large spines on the lateral margins of tergum III of most males.

Remarks. At present, this is the only species known in the genus *Seeversiella.* As such, it is easily recognized by the features discussed in the generic diagnosis and species description. The distinctive secondary sexual characteristics of the male provide the most visible means of recognizing members of this species. However, these vary considerably among males. Some males have very large lateral spines on tergum III and a distinctive and long median carina on tergum VII, while in others these are quite small or, on a very few males, completely absent (compare Fig. 10A–C).

The disjunct nature of the Michigan population is not associated with any obvious structural distinction in comparison with Southwestern populations. While the Michigan specimens are, on the average, a little lighter in color than most Southwestern



Figs. 10–13. *Seeversiella bispinosa,* new species. 10A–10C. Male tergum III from three individuals, showing variation in size of lateral spines. 11. Aedeagus, median lobe. 12. Aedeagus, paramere. 13. Spermatheca.

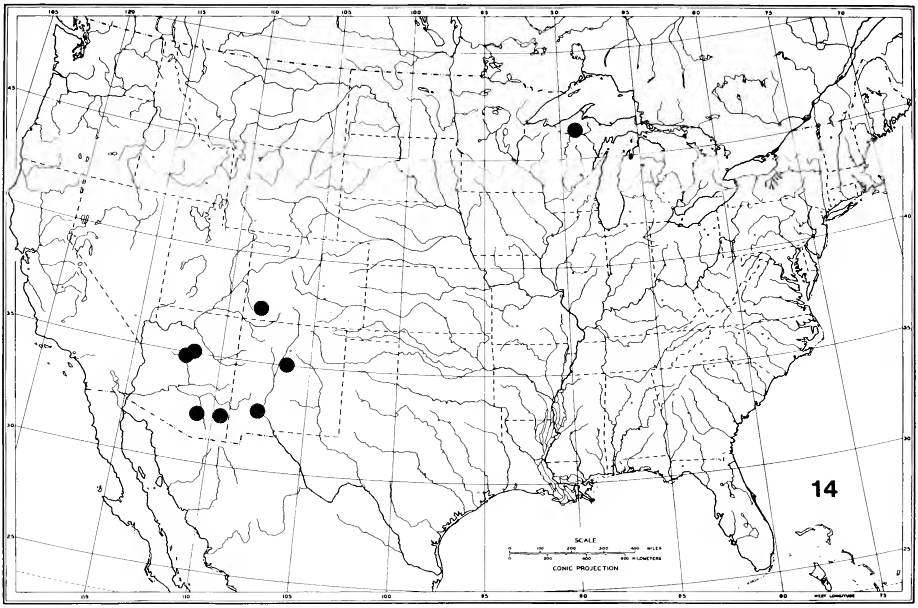


Fig. 14. *Seeversiella bispinosa,* new species. Known distribution.

specimens, they are still well within the range of variation found among specimens from a single large collection in Arizona.

IDENTIFICATION OF *SEEVERSIELLA,* NEW GENUS

The key provided by Seevers (1978) is essentially correct in that it is designed to key out *Seeversiella* at couplet 69, "new genus." However, he misinterpreted the setal pattern on the pronotum, and, therefore, members of *Seeversiella* will fail to agree with either of the alternatives presented in couplet 64. This requires that couplet 64 and several other couplets be rewritten to include more accurate information about members of this new genus and for clarity. This also allows for modification of the confusing triplet in couplet 67. A revised key for couplets 64 through 69 is given below. Couplets which do not differ from those given by Seevers are indicated by "Seevers, 1978."

64(62). Pronotal pubescence patterns with all setae directed caudad or lataerocaudad (Patterns B, fig. 24B–E, or C, fig. 24F–G, Seevers, 1978), or setae directed medially (Fig. 2) 66

– Pronotal pubescence patterns with hairs in midline directed cephalad in at least apical half (Patterns E, fig. 24I, or F, fig. 24J–L, Seevers, 1978) 65

65(64). Seevers, 1978

66(64). Seevers, 1978

67(66). Eye length less than distance from posterior margin of eye to base of head *and* elytra shorter, or only slightly longer than, pronotum, *or* if elytra 1.15–1.2 times as long as pronotum, then pronotal pubescence directed medially 68

– Eye length equal to or greater than distance from base of head, *or,* if eyes smaller, elytra at least 1.2 times as long as pronotum *and* pronotal pubescence directed caudad or laterocaudad 67a

67a(67). Eye length equal to or greater than distance from posterior margin of eye to base of head *and/or* elytra at least 1.2 times as long as pronotum 76

– Eye length equal to distance from posterior margin of eye to base of head *and* elytra only slightly longer than pronotum (less than 1.2 times as long) .... *Anaduosternum* Notman

68(67). Pronotal hypomera broadly visible in lateral aspect; mesocoxal acetabula completely and markedly margined 69

– Pronotal hypomera not visible or partially visible in lateral aspect, if partially visible, then mesocoxal acetabula unmargined or margin very fine and indistinct 71

69(68). Most males with tergum III with latero-apical angles produced as prominent spines (Fig. 10A–C) and male tergum VII with median carina; pronotal pubescence with setae directed medially (Fig. 2) .... *Seeversiella,* new genus

– Males without above combination of secondary sexual characteristics; pronotal pubescence with setae directed caudad or laterocaudad 70

ACKNOWLEDGMENTS

I thank Dr. Rupert Wenzel for reading portions of this manuscript and providing comments and suggestions on historical background. Dr. Alfred Newton, Jr. read and offered helpful suggestions for the entire manuscript. Dr. Lee Herman arranged for loan of specimens from the collections of the American Museum of Natural History, New York. I especially thank Dr. Milton Sanderson for generously donating for study the numerous specimens of this new genus that he had collected in the San Francisco Mountains and surrounding areas of Arizona. His long series provided essential information on intraspecific variation among these beetles. I thank my wife, Aagje Ashe, for inking and otherwise completing the drawings for Figures 1–13.

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Received December 16, 1985; accepted March 13, 1986.

J. New York Entomol. Soc. 94(4):512–515, 1986

FOUR NEW NEOTROPICAL *CEPHALOBYRRHINUS* PIC (COLEOPTERA: DRYOPOIDEA: LIMNICHIDAE)

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Abstract.—Four new species of *Cephalobyrrhinus* are described from Central and South America. They are *C. brevis, C. robustus, C. sedatus,* and *C. lineatus.* The genitalia are figured and a key that will separate the six known species of the genus is included.

Since the publication of my paper on *Cephalobyrrhinus* Pic (Wooldridge, 1977), I have received a number of specimens of the genus from various sources. In addition to extending the ranges of the two known species, the material contained specimens of the following four previously undescribed species. From the ecological data supplied with the specimens it seems clear that the adults of this genus inhabit leaf litter, rotten logs, and decaying vegetation. It is likely that careful collecting in these habitats in tropical regions will reveal still other species.

Cephalobyrrhinus brevis, new species
Fig. 1

Description. Length 1.8 mm, width 1.0 mm, elongate oval, convex. Black to piceous. Head punctation fine on vertex, closer and coarser on front, clypeus alutaceous. Pronotum with fine, even, lightly impressed punctures except for a row of coarse punctures along side margins; tuberculate series fine, even, rugulose. Elytra with small, confused, barely impressed punctures around scutellum; punctures forming vague rows at sides. Prosternal punctation fine. Hypomera shining to slightly alutaceous. Metasternal punctation minute, distant, only slightly closer at sides. Metacoxal plates with fine, lightly impressed punctures. Abdomen polished to faintly alutaceous, punctation fine, only slightly coarser at sides; second sternum with two depressed circular areas to receive metatarsi. Aedeagus with parameres straight and nearly parallel-sided; penis narrow and tapering evenly to a rounded, acute tip (Fig. 1).

Holotype ♂ and *allotype* ♀. Ecuador, Napo. 600 m (20 km S Tena) VII.11.1976. S. Peck (FMNH).

Paratypes. Ecuador, Napo. 16 spec. Same data as holotype (12 FMNH, 4 USNM); 11 spec. 250 m el., Limoncocha, VI.21.1976. Bactris-spiny palm (FMNH).

Cephalobyrrhinus robustus, new species
Fig. 2

Description. Length 3.2 mm, width 1.9 mm, ovate, convex. Black. Head punctation fine and distant on vertex, clypeus alutaceous with close punctures. Pronotum with minute, perforate punctation, tuberculate row short and rugulose. Elytra with seven long and two short longitudinal rows of deep, coarsely impressed punctures close enough to form partial grooves on disk; punctation near scutellum small. Prosternum finely punctate; process with a broad, shallow longitudinal sulcus. Hypomera polished, minutely punctate. Metasternum with coarse punctation, punctures largest on posterior half near midline; metacoxae finely punctate with a few larger punctures at sides. Abdomen finely alutaceous, finely punctate except polished in circular areas on each side of second sternum to receive tarsi. Parameres of aedeagus parallel-sided, evenly curved, diverging from about the middle, tips rounded; penis short, broad, tapering to a rounded tip (Fig. 2).

Holotype ♂ and *allotype* ♀. Peru. 43 mi E Tingo Maria, 1,300 m, XI.18.1954. E. I. Schlinger and E. S. Ross (CAS).

Paratypes. Ecuador, Napo, 3♀, Limoncocha, 10 July 1977, W. E. Steiner (USNM). Pastaza, 1 spec. Cusuimi, Rio Cusuimi, 150 km SE Puyo, 320 m, VII.1–2.1971. B. Malkin (FMNH). Peru, 5 spec. same data as holotype.

Cephalobyrrhinus sedatus, new species

Fig. 3

Description. Length 2.9 mm, width 1.6 mm, elongate oval, convex. Black. Head punctation small, clypeus alutaceous, punctures becoming fine behind epistomal suture. Pronotal punctation small, scattered, becoming coarser and closer along lateral margins; tuberculate series short and irregular. Elytra with three long rows and one short row of broad, coarse punctures at sides and a short row past middle along suture; disk flat with small, scattered punctures, punctures obsolete around scutellum. Prosternum with small, scattered punctation; process broad, somewhat flattened. Hypomera alutaceous. Metasternum polished with minute, scattered punctures; metacoxal plates microreticulate with small, scattered punctures. Abdomen faintly microreticulate with minute punctation, except polished in circular areas on each side of second sternum to receive tarsi. Aedeagus with outer margins of parameres converging to rounded tips; penis broad, tapering abruptly to an obtusely rounded tip (Fig. 3).

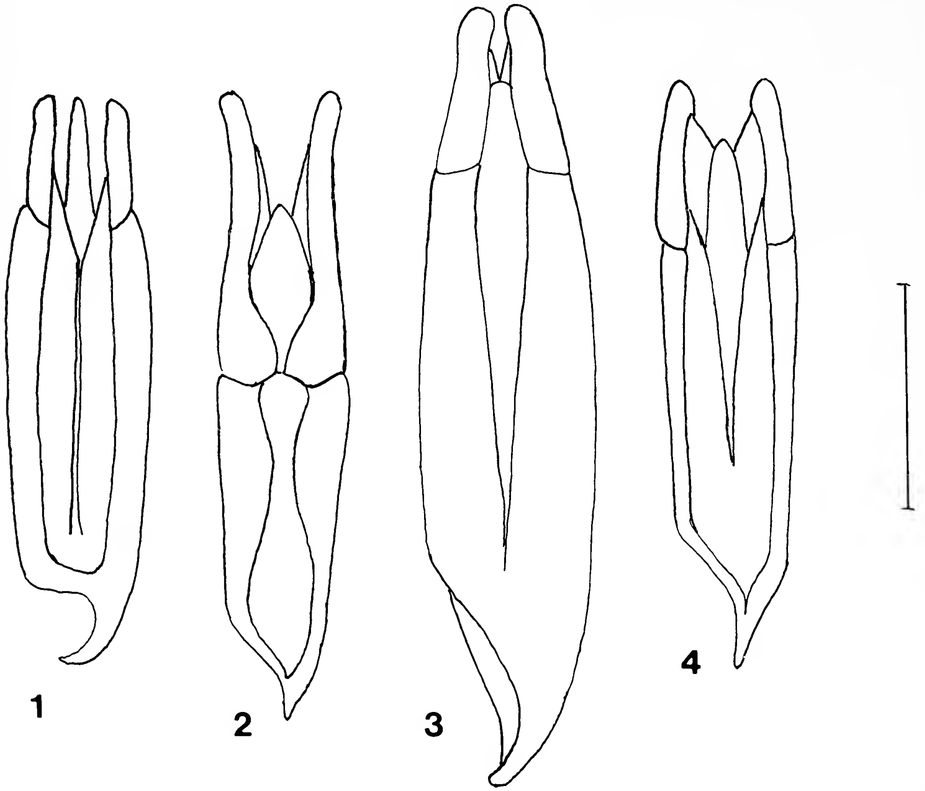
Holotype ♂ and *allotype* ♀. Ecuador, Pichincha. 6 mi W Santo Domingo de los Colorados II.23.55, E. I. Schlinger and E. S. Ross (CAS).

Paratypes. Ecuador, Pich. 7 spec. Same data as holotype (5 CAS, 2 DPWC). 3 spec. 47 km SE Santo Domingo, Rio Palenque Sta., II.22–28.1976, 300 m, S. M. Campbell (CNC).

Cephalobyrrhinus lineatus, new species

Fig. 4

Description. Length 2.0 mm, width 1.0 mm, narrowly elongate, parallel-sided, convex. Black to piceous, ventral surfaces dark red-brown. Head punctation fine, clypeus alutaceous with larger punctures. Pronotum with fine punctation on disk, coarser at sides; transverse tuberculate line very fine, more rugulose than tuberculate. Each elytron with seven rows of linear punctures on disk and two shorter incomplete series at sides, punctures distinct but not deeply impressed; scutellar row distinct; only sutural row extended past elytral declivity. Prosternal punctation fine, distant. Hypomera alutaceous. Metasternum with coarse, broad punctures at sides and around



Figs. 1–4. Dorsal view of aedeagus. 1. *Cephalobyrrhinus brevis.* 2. *C. robustus.* 3. *C. sedatus.* 4. *C. lineatus.* Line equals 0.2 mm.

crural depressions, becoming fine and distant at midline. Metacoxal plates with large, coarse punctures. Abdomen polished between punctures which are larger at sides than at midline; second sternum with two nearly circular, slightly depressed, nearly impunctate areas to receive metatarsi. Aedeagus with parameres parallel-sided and rounded at tips; penis narrow, nearly parallel-sided, evenly rounded at tip (Fig. 4).

Holotype ♂ and *allotype* ♀. Panama, Canal Zone, Barro Colorado Is. II.6.1976, A. Newton. Litter under rotten logs (MCZ).

Paratypes. Costa Rica, 7 spec. Heredia, OTS La Selva Field Sta., Puerto Viejo de Sarapiqui, Rio Puerto Viejo, III.11.1973, J. Wagner, J. Kethley (FMNH); 6 spec. Puntarenas, OSA Peninsula, 5 km W Rincon de OSA, III.24.1973, bat guano inside hollow log, J. Werner, J. Kethley (FMNH); 2 spec. same data except III.25.1973 (FMNH); 7 spec. same data except forest floor, III.30.1973 (FMNH). Panama, 3 spec. Bocas del Toro, Almirante, trail to dam on Nigua Cr. III.25.1951, H. S. Dybas (FMNH); 1 spec. same data except III.31.1959 (FMNH); 5 spec. same data as holotype (MCZ); 9 spec. same data as holotype except II.13.1976 (MCZ); 5 spec. same data as holotype except II.17.1976 (MCZ); 6 spec. Canal Zone, Achiote Rd. 9 mi

SW Gatun, VI.19.76. A. Newton (MCZ). 1 spec. Panama, Cerro Campana 3,200 ft II.1976, A. Newton (MCZ).

KEY TO THE SPECIES OF *CEPHALOBYRRHINUS*

1\. Pronotal series of tuberculate punctures broad and irregular, punctures greatly raised (Mexico to northern Venezuela) .... *curticornis* Pic

– Pronotal series of tuberculate punctures narrow, punctures often minute and rugulose in appearance 2

2(1). All metasternal punctation fine and even 3

– Metasternal punctation varying from minute to coarse and broad 4

3(2). Prosternal row of tuberculate punctures short and irregular; size greater than 2.75 mm (Ecuador) .... *sedatus,* n. sp.

– Prosternal row of tuberculate punctures straight; size less than 2.0 mm (Ecuador) .... *brevis,* n. sp.

4(2). Metasternal punctation distinctly larger at sides 5

– Metasternal punctation distinctly larger in central portion, leaving a finely punctate area behind crural cavities and in front of metacoxae; size large, over 3.0 mm (Ecuador & Peru) .... *robustus,* n. sp.

5(4). Several rows of elytral punctures continuing past declivity (Ecuador, Bolivia & Peru) .... *impressopunctatus* Wooldridge

– Only the sutural row of elytral punctures distinct past declivity (Costa Rica & Panama) .... *lineatus,* n. sp.

ACKNOWLEDGMENTS

Thanks are due to the following individuals and institutions for the loan of material. The abbreviations are those used to indicate distribution of type material and in general this corresponds to the source of the material.

D. H. Kavanaugh, California Academy of Sciences, San Francisco, Calif. (CAS); A. Smetana and L. LeSage, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ont. (CNC); H. Nelson, Field Museum of Natural History, Chicago, Ill. (FMNH); M. Thayer and A. Newton, Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (MCZ); and P. J. Spangler, National Museum of Natural History, Washington, D.C. (USNM). Those specimens labelled DPWC are retained in the author's collection.

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Received December 6, 1985; accepted April 9, 1986.

J. New York Entomol. Soc. 94(4):516–525, 1986

REDISCOVERY AND SPECIES STATUS OF THE NEOTROPICAL SWALLOWTAIL BUTTERFLY *PAPILIO ILLUMINATUS* NIEPELT (LEPIDOPTERA: PAPILIONIDAE)

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Abstract.—Protesilaus illuminatus (Niepelt), unrecorded since its 1928 description, is given species status based on study of recent specimens from the Rio Putumayo valley of Colombia, syntypical material and wing and genitalic characters of congeners. A lectotype is designated.

For several years a reputedly undescribed swallowtail butterfly belonging to the group *Eurytides* sens. lat. was reported to be circulating on the commercial butterfly market. Taxa of this group "differ . . . widely in adult external appearance" (Munroe, 1961) making unidentifiable specimens of particular interest to collectors and commercial dealers. Photographs of two of five reported specimens of this taxon (Fig. 1A–C) had been sent from commercial dealers to at least two scientific institutions (Allyn Museum of Entomology [AME], Lee D. Miller, pers. comm., and British Museum, Natural History [BMNH], second author, pers. comm.) and two collector/appraisers (the second and third authors) for confirmation of this apparent undescribed status. These two specimens had been obtained in 1981 by Mr. Jerry Schlommer, a commercial dealer, from local collectors on the Rio Putumayo, Colombia. The butterflies were characterized by three large white triangular patches on the hindwing upperside, contrasting the markings of known congeners which display either (1) patches over the entire surfaces of one or both wings (Fig. 1D) or (2) variously large red and/or white elipses or dots on this area of the wing (Fig. 1E). From the photographs, Miller and the second and third authors confirmed the apparent uniqueness of these specimens to their owners. Until recently, however, none of the specimens was available for scientific study. In 1985, Mr. Rozycki purchased and donated the photographed specimens for taxonomic study. Subsequently, during review of data assembled in this study Dr. Keith S. Brown (Dept. of Zoology, Universidade Estadual de Campinas, São Paulo, Brazil), who is preparing a synonymic list of Neotropical Papilionidae, discovered that, despite the brevity of a 1928 original description, a syntype of *Papilio gayi* [sic] *illuminatus* Niepelt extant in the Museu National (MNR), Rio de Janeiro, Brazil (Fig. 2A, B) seemed nearly identical to the AMNH assembled specimens. As a result, our eventual study concerned both the status and affinities of the AMNH Rio Putumayo specimens and that of *illuminatus,* which had apparently not been referred to in the scientific literature since its original description (Beattie, 1976).

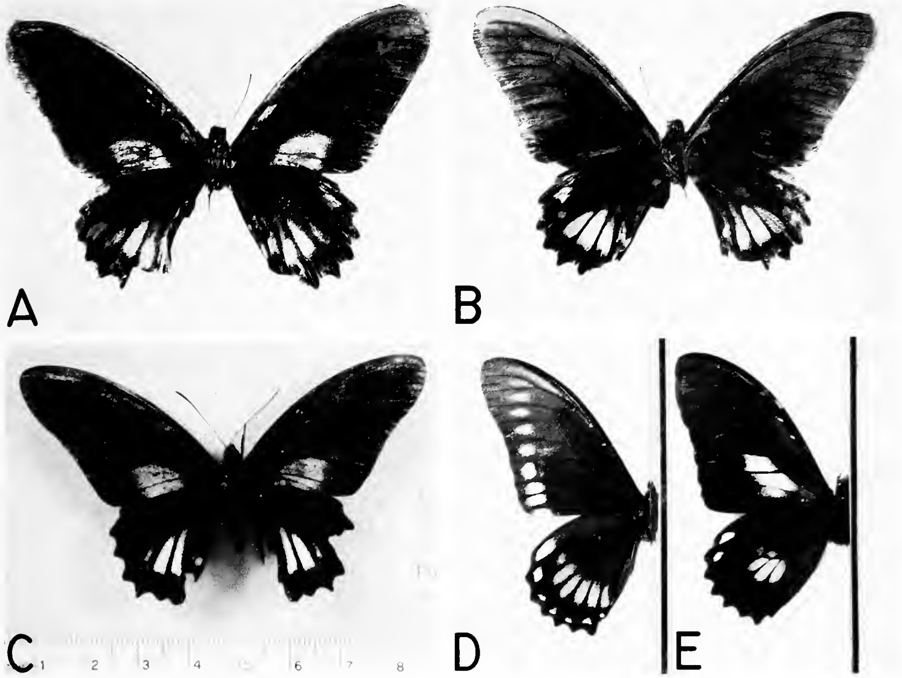

Fig. 1. Specimens of *Protesilaus illuminatus* caught in 1981 in the Rio Putumayo valley, Colombia, A–C (A–B, upper surface; C, under surface). D. *P. phaon* (Colombia, AMNH), a banded taxon. E. *P. euryleon* (Balzabamba, Ecuador, AMNH), a taxon with red hindwing orbs.

TAXONOMIC ANALYSIS

Both Munroe (1961) and Hancock (1983) placed taxa with the combinations of wing marking mentioned above in a "*Lysithous*-related group" of *Protesilaus* (hereafter "*Protesilaus*"), Munroe placing *Protesilaus* as a subgenus of *Eurytides,* Hancock giving the former full generic status. Irrespective of this difference both authors included the following taxa in the group: *pausanias* (Hewitson), *protodamas* (Godart), *microdamas* (Burmeister), *phaon* (Boisduval), *chibcha* (Fassl), *euryleon* (Hewitson), *hipparchus* (Staudinger), *harmodius* (Doubleday), *trapeza* (Rothschild and Jordan), *xynias* (Hewitson), *ariarathes* (Esper), *ilus* (Fabricius), *branchus* (Doubleday), *belesis* (Bates), *thymbraeus* (Boisduval), *lysithous* (Hübner), *kumbachi* (Vogeler), and *asius* (Fabricius). The outstanding wing morph differences amongst these taxa can be summarized as follows. All are untailed mimics of Troidini (Papilionidae) or Heliconiinae (Nymphalidae) except tailed *thymbraeus, lysithous* and *asius.* Of those untailed, all have mostly red (but sometimes white) circular or elliptical upperside-hindwing markings (Troidini mimics) except (1) *phaon, protodamas* and *microdamas* which have white, yellow-green (or these red-tinted) bands and (2) *pausanias* and a *protodamas* form which have a broad median yellow patch on the forewing (Heliconiinae mimics).

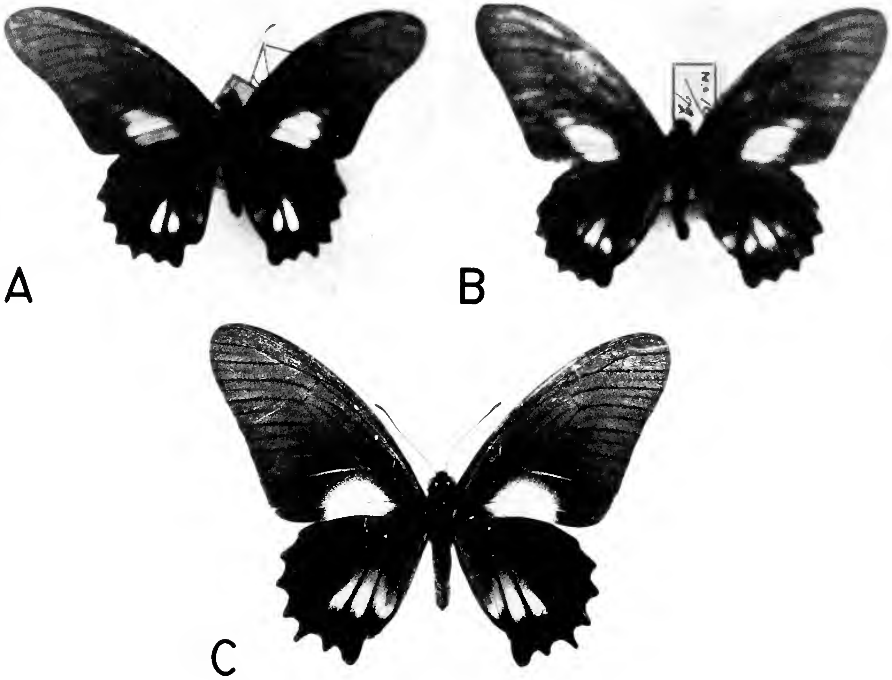

Fig. 2. A. Lectotype male, *P. illuminatus* (MNR), upper surface; B. Allotype female, *P. illuminatus* (MNR), upper surface; C. *P. ariarathes gayi* (Janjui, Peru, AMNH) with red triangular hindwing patches otherwise shaped like those of *illuminatus.*

Munroe (1961) and Hancock (1983) emphasized characters of the male valval harpe in distinguishing taxa of this group. Beutelspacher and Howe (1984) illustrated differences in the valvae which diagnose taxa of *Eurytides* sens. lat. occurring in Mexico. We have studied the male genitalia of *Protesilaus* taxa and in Figures 3–5 illustrate valvae of twenty-one taxa, summarizing our comments on characters in the following REMARKS. When compared to all *Eurytides* and *Protesilaus* taxa, male genitalia of species of tailless *Protesilaus* are relatively alike. However, among them five general subgroups are recognizable. These subgroups correspond closely with the arrangement of D'Abrera (1981) based on wing pattern. Accordingly, for purposes of this paper and in concurrence with group names suggested by Dr. K. S. Brown (pers. comm.) we treat these as follows, citing D'Abrera (1981) plate numbers first, followed by our figure numbers: the "*phaon*" cluster (pp. 62–63) (Fig. 3); the "*harmodius*" cluster (pp. 64–65) (Fig. 4); the "*ariarathes*" cluster (pp. 66–67 [top]) (Fig. 4); the "*belesis*" cluster (p. 67 [bottom]) (Fig. 5), and a possibly previously unrecognized cluster consisting of *microdamas* (figured alone by D'Abrera, p. 63) (Fig. 5), *P. dospassosi* (Rütimeyer) and possibly *P. huanacana* (deLuque) (Johnson, Matusik and Rozycki, 1986). None of these two latter taxa was included in *Protesilaus* by D'Abrera (1981) or Hancock (1983) due to the taxa being either little-known or misdiagnosed pending dissection (*dospassosi* as a *Heraclides sensu* Hancock, 1983). Significantly, male genitalia of *P. microdamas* differ from all other tailless *Protesilaus* in lacking the ventrad protruding process of the mesio-ventral surface of the valval harpe (*sensu* Munroe, 1961). The type of *P. dospassosi* and some specimens otherwise like *P. huanucana* also lack this process (Johnson, Matusik and Rozycki, 1986). It is generally considered (Hancock, 1983, and pers. comm., K. S. Brown, pers. comm.) that the taxa *kumbachi* and *chibcha* are aberrations of *P. lysithous* and *P. euryleon,* respectively. They are, therefore, not given further consideration in this paper pending an effort by us to locate their types.

As predictable from wing characters, genitalia of the AMNH Rio Putumayo specimens (Fig. 3G) indicate association with the *phaon* cluster. However, these specimens, the *illuminatus* syntype (MNR, extant of three original syntypes) and one additional MNR female *illuminatus* (Figs. 1A–C, 2A, B) are intermediate in wing pattern between the variously banded *phaon*-like taxa (Fig. 1D) and the red-spotted *euryleon*-like taxa (Fig. 1E). This characteristic, which caused lepidopterists to initially regard the Rio Putumayo specimens as undescribed, is further significant because current taxonomic usage would consider any non-red *Protesilaus* from the Rio Putumayo valley as a *P. ariarathes* mimicking unusual white-marked *Parides* known to occur there (K. S. Brown, pers. comm.). Association of *illuminatus* with *ariarathes* is consistent with Niepelt's original designation of the taxon as "*Papilio gayi* Lucas *illuminatus* Niep. n. subsp." (Niepelt, 1928, p. 390). The taxon *gayi* has since been consistently viewed as a subspecies of *ariarathes* (Rothschild and Jordan, 1906; D'Almeida, 1965; D'Abrera, 1981). In Figure 2C we illustrate an unusual male *ariarathes gayi* (confirmed by genitalic dissection [Fig. 4D]) which has triangular hindwing markings like *illuminatus* but which are red, not white. Overall assessment of the characters of *illuminatus* has led us and Brown to concur that *illuminatus* is a taxon of the *phaon* species cluster and either a distinct species (our view) or in the opinion of Brown a distinct species, or a subspecies of *euryleon.* Given the disparity of the wing pattern of *illuminatus* from *euryleon,* the consistent morph in both males and females of *illuminatus,* and the latter's male genitalia, we propose the following:

Protesilaus illuminatus (Niepelt), **New Combination**, **Revised Status**
Figs. 1A–C, 2A, B, 3G

Papilio gayi illuminatus Niepelt, 1928, Int. Entom. zeitschr. 21:390.

Diagnosis. Compared to all other *Protesilaus* readily recognized by three distinct white to cream triangular patches on the hindwing upperside in cells CU_2, CU_1 and M_3 and a red patch between these and the anal angle. Underside of hindwing similar but with additional red dot postmedian in cell M_2. In the genitalia distinguishable from all congeners by the dorsal surface of the valval harpe ("keel" *sensu* Johnson, Matusik and Rozycki, 1986) with reduced size caudad, serrated ridge ventrad nearly straight, and markedly large rhomboid-shaped sclerotized area ventrad on the clasper with very elongate ventrally protruding process along the ventral angle (*sensu* Hancock, 1983; Munroe, 1961).

Description. MALE. Upperside of wings: Ground color, both wings, brownish black. Forewing with dull yellow-cream patch in median area from below discal cell

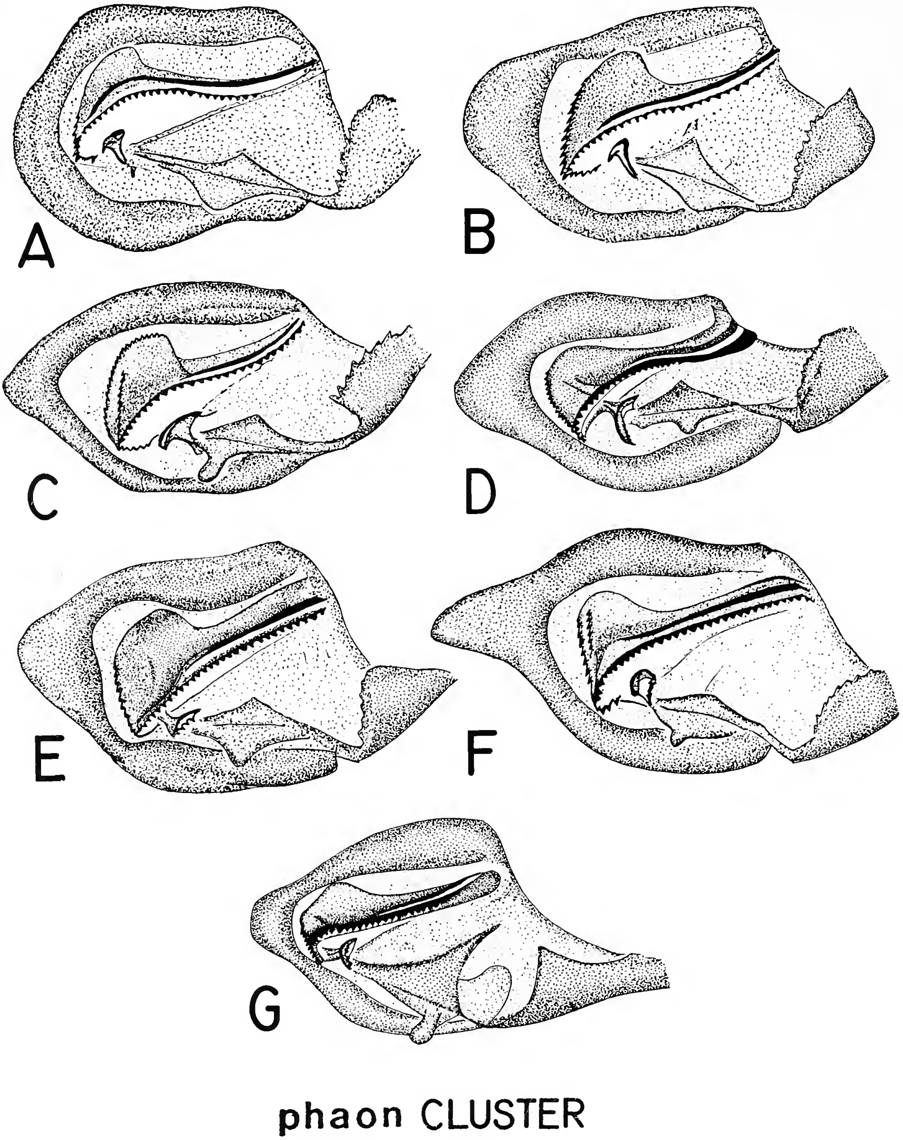

Fig. 3. Genitalia of the "*phaon* cluster" (number of dissections, parentheses). A. *pausanias,* Jepelacio, Peru (3); B. *protodamas,* Gavea, Brazil (3); C. *phaon,* Colombia (3); D. *euryleon euryleon,* Costa Rica (3); E. *euryleon haenshi* (Rothschild and Jordan), Balzabamba, Ecuador (3); F. *euryleon pithonius* (Rothschild and Jordan), Cauca Valley, Colombia (3); G. *illuminatus,* Rio Putumayo valley, Colombia (2).

to inner margin. Hindwing with three long triangular yellow-cream patches postmedian to postbasal in cells CU_2, CU_1 and M_3. Large red patches between vein 2A and the anal margin. Slight red spots distad each white triangular patch, postmedian from cells CU_2 to M_2. No tail. Underside of wings: As on upperside but with red dot postmedian in cell M_2 and vivid red at the juncture of wing bases and thorax. Length of forewing 42.0 mm (AMNH male); 38.5 mm Rozycki male.

FEMALE. Upperside of wings: Compared to male, wing shape broader and wing length longer (Fig. 2B); hindwing, anal red spot larger, white postmedian bands more expansive costad, invading cell M_3. Forewing, median cream-white patch more expansive costad, invading cell M_3. Underside of wings: Photograph not available. Forewing length: Unavailable.

Male genitalia (Fig. 3G). Caudal "head" of dorsal surface of valval harpe ("keel" *sensu* Johnson, Matusik and Rozycki, 1986) reduced, ventrad serrated ridge nearly straight. "Mesially directed process" (*sensu* Hancock, 1983; Munroe, 1961) extremely narrow and elongate; rhomboid-shaped ventrad sclerotized areas of clasper far larger dorsad than on sister taxa and with prominent ventrally protruding process at ventral angle (*sensu* Hancock, 1983; Munroe, 1961).

Female genitalia. Unknown.

Type. We designate the syntype (Fig. 2A) (MNR), labelled "type *gayi illuminatus* Niepelt, Mocoa, S. Colombia, Oct. 1927, Col. Julius Arp" as lectotype. Location of remaining two syntypes of original description is unknown. Also, we designate the female (Fig. 2B) labelled "*gayi* Luc., [illegible], Col.," as the "designated allotype" *sensu* Smith, 1983. We have requested K. S. Brown to affix labels to this effect. Regarding additional specimens, see REMARKS.

Distribution. Rio Putumayo valley of southern Colombia.

Remarks. Protesilaus "lysithous group" taxa exhibit a single-layered valval harpe (dark, keel-like structure centrad in Figs. 3–5) with a laterally extending spike associated ventrad and a variously rhomboid structure cephalo-ventrad which has a ventrally extending process. The closely related "marcellus Group" (*sensu* Munroe, 1961) displays a harpe of two parallel layers (a keel beneath a keel) without an emphatic spike and without a ventrally extending process. The keel-like structure in Figures 3–5 consists ventrad of two closely parallel high ridges (drawn in thick solid black) separated by a deep fissure (shown in white or very light gray). The ventrad ridge is variously dentate. The keel can terminate caudad with a variously expressed "head": characteristically single-edged and serrate, double-edged and serrate, or non-serrate in particular species clusters. The laterally pointing spike can be characteristically pointed, furcate, or conical; the ventral process of the rhomboid structure is variously emphatic. Characters of the keel are most useful with features of the lateral spike and ventral process being less reliable but distinctive in some taxa. Exception to the above general configuration occurs in the "*microdamas* cluster," whose taxa have the characteristic keel on the harpe but have a generally caudad-pointing spike and no ventral process. Subject to much intraspecific variation, the less sclerotized areas of the valval clasper surrounding the harpe do not appear diagnostically useful for the groups.

Characters generally diagnostic for each of the species clusters are—"*phaon* cluster": keel with moderately enlarged head and faint to moderate evidence of a double-edge, each edge evidencing serration or at least a second incline toward the parallel

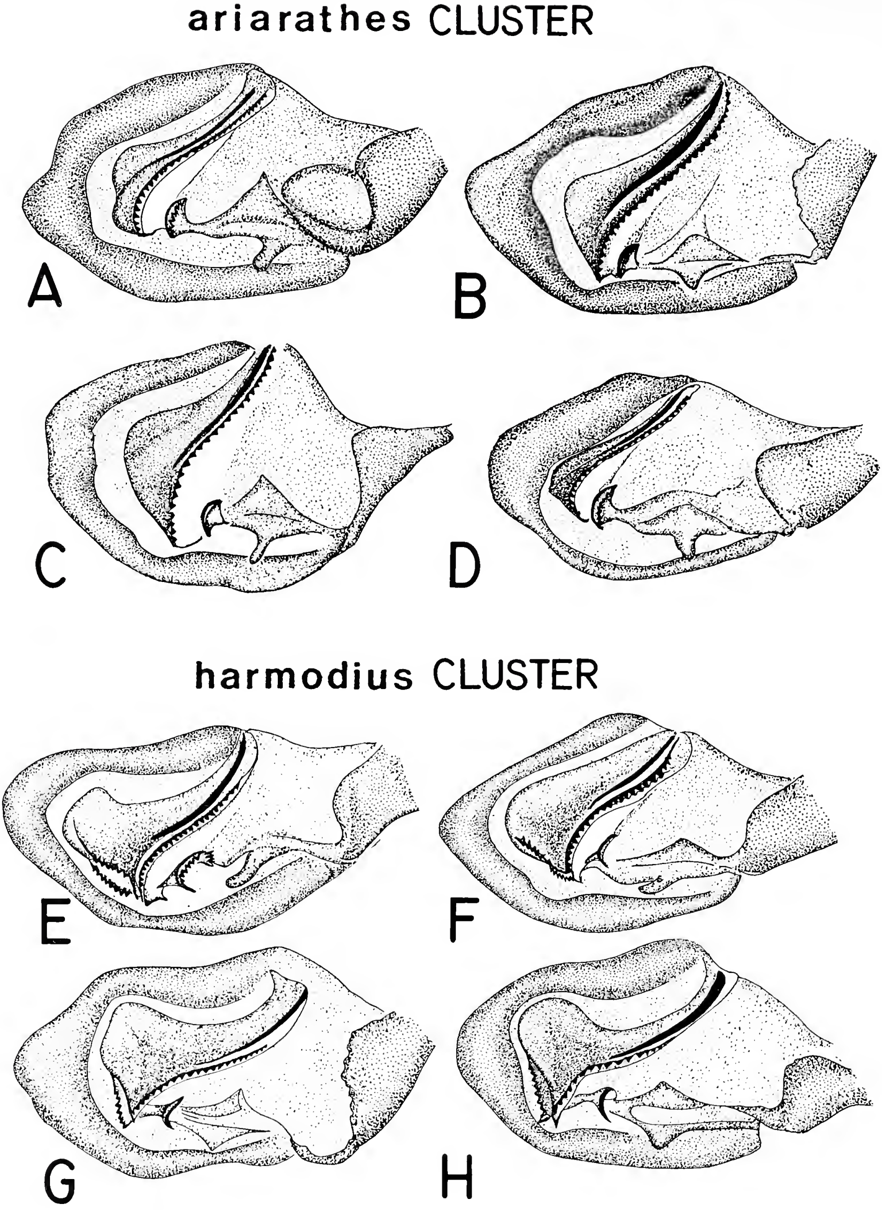

Fig. 4. Genitalia of the "*ariarathes* cluster" (A–D) and the "*harmodius* cluster" (E–H) (number of dissections, parentheses, other localities, brackets). A. *ariarathes ariarathes,* French Guiana (3); B. *ariarathes gayi* f. *cyamon* (Grey), Middle Rio Ucayali, Peru (3), Alto Jurua, Brazil (1) [additional studied: *gayi gayi,* Janjui, Peru (1), Buena Vista, Bolivia (1); *gayi metagenes* (Rothschild and Jordan), Mt. Duida, Venezuela (1)]; C. *ariarathes menes* (Rothschild and Jordan), Tukeit, Guyana (3); D. *ariarathes* of Figure 2C, Janjui, Peru; E. *harmodius harmodius,* Bolivia (3); F. *harmodius xenaides* (Hewitson), Rio Pastaza, Ecuador (3); G. *trapeza,* Rio Napo, Ecuador (3); H. *xynias,* Rio Santiago, Peru (3).

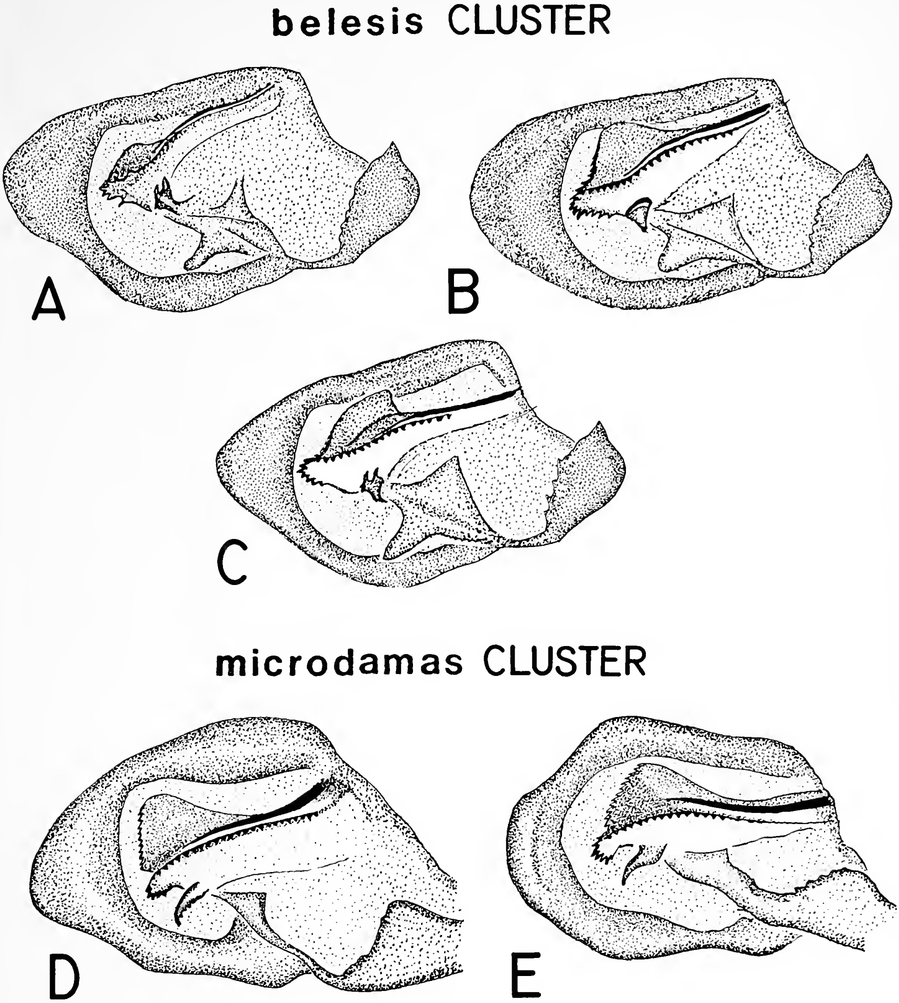

Fig. 5. Genitalia of the "*belesis* cluster" (A–C) and "*microdamas* cluster" (D, E) (number of dissections, parentheses). A. *belesis,* Soyolapan, Mexico (3); B. *branchus,* San Jeronimo (Chiapas), Mexico (3); C. *ilus,* Sosumuco, Colombia (3); D. *microdamas,* Sapucay, Paraguay (5); E. *dospassosi* (holotype), Rio Putumayo, Colombia.

ridges; lateral process generally conical; ventral process variously emphatic; "*harmodius* cluster": head of keel extremely enlarged and usually severely angled; double-edge distinct with both surfaces heavily serrate; lateral process conical, thin-edged and extremely arc-shaped terminad; ventral process variously expressed as generally small rhomboid structure; "*ariarathes* cluster": keel smoothly inclined with generally moderate to diminutive head, single-edged and generally non-serrate; lateral process conical with the angle of its arc positioned closely parallel to that of the keel (very noticeable in the dissections, lateral processes of other taxa clusters being variously at odd angles to the keel); rhomboid structure small, with the ventral process usually narrow to pronounced; "*belesis* cluster": keel curved irregularly ventrad with caudad dentate areas flared notably outward; head variously serrate, single-edged, often inclined laterally; lateral process furcate in two taxa, conical in the third; rhomboid structure moderately large with ventrad process very emphatic and often wide; "*microdamas* cluster": no ventral process, rhomboid structure occurring only dorsad; caphalo-ventral "shoulder" connects clasper to vinculum widely adjoined to ventrad areas of the clasper; keel variously inclined or with an emphatic head, single-edged and serrate caudad; lateral process thinly pointed and angled markedly dorsad.

Nine specimens of *P. illuminatus* are known or have been reported in the literature. These are as follows: Niepelt (1928) three syntype males; MNR, one female; AMNH, one male; and R. Rozycki collection (Chicago, Illinois), one male. The remaining three specimens are males in the possession of a commercial dealer who wishes to remain anonymous. These have been examined and identified by the third author. The last five specimens mentioned above have been collected since 1981. This apparent rarity is not unusual among Neotropical Papilionidae. For example, Johnson, Rozycki and Matusik (1985) confirmed only seventeen known specimens of *Pterourus xanthopleura* (Godman and Salvin) in thirteen major United States, European and South American museums. Only three of these specimens are in South American collections. *P. xanthopleura* is a well-known swallowtail butterfly, popular with collectors and commercially sought after. The above persons also located only three specimens of *P. diaphora* (Staudinger), the sister species of *xanthopleura.* Apparent scarcity, therefore, or limitation to a localized habitat should not prejudice the apparent species status accorded *illuminatus.* There are numerous Papilionidae species which are known from, or at least only collectable at, particular limited locales (*Battus zetides* Munroe, *B. streckerianus* Honrath, *Heraclides moroni* [Moreau], D'Abrera, 1981).

ACKNOWLEDGMENTS

Numerous specialists and museum curators aided in discussing data, reviewing manuscripts or searching various collections. Below, we list these persons, noting after each the collection surveyed: Dr. Keith S. Brown (collection Universidade Estadual de Campinas, Sao Paulo, Brazil; Museu Nacional, Rio de Janeiro, Brazil; Collection Museo de Historia Natural "Javier Prado," Lima, Peru); Dr. Tommaso Racheli (Collection Instituto de Zoologia Agricola, Maracay, Venezuela; Collection Tommaso Racheli); Dr. Ernesto W. Schmidt-Mumm (Collection Ernesto W. Schmidt-Mumm); Dr. Olaf H. H. Mielke (Collection, Dep. de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil); Dr. Lee D. Miller (Allyn Museum of Entomology of the University of Florida, Sarasota, Florida, U.S.A.); Dr. H. T. Hannemann (Zoologishes Museum der Humbolt Universität, Berlin, Germany); Dr. Rienk de Jong (Rijkmuseum van Natuurlijke Historie, Leiden, Netherlands); Dr. John H. Rawlins (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A); Dr. Robert K. Robbins (National Museum of Natural History, Washington, D.C., USA); Richard Vane-Wright (British Museum, Natural History, London, United Kingdom). Dr. Keith brown kindly reviewed drafts of the manuscript as well as suggested and/or contacted for us numerous of the above listed workers or collections. We are most grateful for his generous assistance. The following persons discussed this project with us, and/or reviewed manuscripts or materials: Dr. Ernesto W. Schmidt-Mumm, Dr. Tommaso Racheli, Dr. David

L. Hancock (National Museum, Republic of Zimbabwe, Bulawayo, Zimbabwe). Two anonymous reviewers made very helpful comments and Dr. Randall T. Schuh (AMNH) made numerous helpful suggestions concerning methods and procedures. Dr. Frederick H. Rindge (AMNH) kindly has faciliated access to AMNH papilionid holdings for the second and third authors.

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Received June 4, 1985; accepted April 24, 1986.

J. New York Entomol. Soc. 94(4):526–530, 1986

THE LIFE HISTORY OF *TATOCHILA DISTINCTA DISTINCTA,* A RARE BUTTERFLY FROM THE *PUNA* OF NORTHERN ARGENTINA (LEPIDOPTERA: PIERIDAE)

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Abstract.—Tatochila distincta distincta is a very rare pierid found above 3,000 m in the *puna* of far northern Argentina. Its egg, larva, pupa and aspects of its behavior and ecology are described. All are similar to other *Tatochila* heretofore described and support the previously postulated close affinity of the *xanthodice* and *sterodice* species-groups.

This is the fifth in a series of papers describing the preparatory stages of the Pierini of the Andean region. The largest pierine genus in the Andes is *Tatochila* Butler, which was monographed by Herrera and Field (1959). *Tatochila* includes five species-groups, of which at least some information on life history is now available for three: the *xanthodice* Lucas group (Shapiro, 1978) and the *sterodice* Stgr. and *autodice* Hbn. groups (Shapiro, 1979). *Tatochila distincta* Jörgensen is one of the rarest and least-known members of the genus. It was described from the Province of Catamarca, northwestern Argentina (Jörgensen, 1916); additional specimens known to Herrera and Field were from the adjacent Province of Tucumán, as well as one from Puno, Peru, which they regarded as dubious but which probably represents a subsequently described subspecies which is widespread in southern Peru. Herrera and Field placed *distincta* with *xanthodice* in their Group E based on genital morphology—specifically aedeagal shape, which, they noted, approximated the condition in the genera *Hypsochila* Ureta, *Phulia* Herrich-Schaeffer, and *Piercolias* Stgr. This assignment—based as it is on a single character, in a group where parallelisms are rampant—has always seemed tenuous, especially since the habitus of *distincta* is so different from *xanthodice* and its range so widely disjunct from that north-Andean species. There have been no published natural-history observations on *distincta* since Jörgensen wrote: "This very interesting species appears to have a very limited distribution. I have hunted it only in some localities of the Aconquija range: Cerro Negro, 3500m; Cerro de la Ensenada, 3200m; La Ollada, 3100. It flies in the months of February and March in the windiest and most sun-bathed gorges and summits, especially in the morning, usually in the company of *macrodice.* When the sun goes in it flies no more . . . ."

Tatochila distincta distincta occurs in the bleak high plateaus, or *puna,* of the Provinces of Salta and Jujuy in northern Argentina near the Bolivian border. It is greatly outnumbered by *T. sterodice macrodice* Stgr., with which it usually flies. On 7 February 1985 a female was collected near Tres Cruces, Province of Jujuy, at 3,800 m. She oviposited freely on *Brassica campestris* L. which was collected from vegetable gardens in the Quebrada de Humahuaca on the trip down to the city of San Salvador de Jujuy, and the eggs were transported to Davis, California where the larvae were reared on *B. nigra* (L.) Koch. and *B. kaber* (DC.) Wheeler. Rearing was on cuttings in cardboard cylinders 21 × 11 cm with transparent mesh tops under 10L:14D, 23.9°/12.8°C in growth chambers. Preserved early stages are being retained at Davis at this time for comparative studies of chaetotaxy and development. Color descriptions were prepared from life. Those in parentheses refer to the system of Kornerup and Wanscher (1978).

DESCRIPTIONS

Egg (Fig. 1). Erect, fusiform, 1.15 × 0.38 mm, the chorion sculptured as figured, with about 11 vertical and about 53 horizontal ribs. Light orange (5A5) when laid, becoming slate-gray about 12 h before hatching. Laid singly on leaves and stems of leafy Crucifers in captivity, not observed afield. The larva eats its eggshell after hatching, as is usual in *Tatochila.* Time to hatch, 5 days.

Larva: First instar (Fig. 2). At hatch 1.5 mm. Dull ochre ("grayish orange," 5B3) with black head, apparently unmarked except for numerous minute tubercles bearing short setae; turning gray-green ("ash blonde," 3C3) after feeding. Feeds by excavating pits in leaves and flower buds. Length of instar, 3 days.

Second instar. After molt 4 mm. Gray-green (3C3) with a faint dorsal line and subdorsal and stigmatal stripes, all yellow (4A5, "butter yellow"). Head blackish to slate gray (4F2, "smoke brown"), venter gray-green (3D2, "yellowish gray"). Length of instar, 4 days.

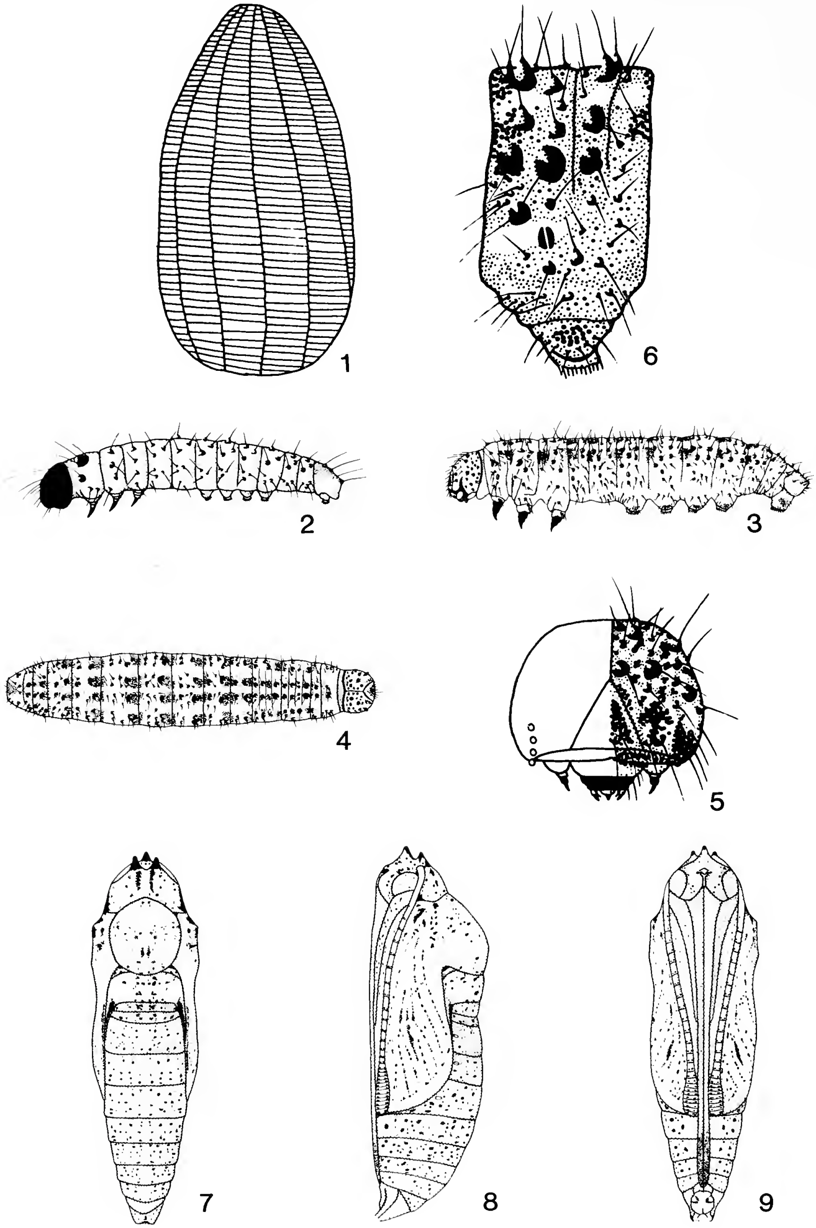
Third instar. After molt 7 mm long at rest. Similar to second instar, with a distinct orange "collar" behind the head (8A8, "orange red"). The larva feeds actively on the aerial parts of the plant, and when not feeding sits lengthwise on the stem. Length of instar, 5 days.

Fourth instar. After molt 11 mm. Slate gray (4F2) with black tubercles, the dorsal and subdorsal stripes distinct, bright yellow (4A5, "butter yellow"), collar orange as before, head slate gray mottled with black; venter gray-green (3D2, "yellowish gray") seemingly finely irrorated with black and pale yellow. Length of instar, 5 days.

Fifth instar (Figs. 3–6). After molt 18 mm, reaching 30 mm at maturity. Body with many black tubercles in 3 sizes, each bearing a short whitish hair. Head slate gray, mottled with black, ocelli black; body slate gray, the dorsal and subdorsal stripes distinct, the subdorsals wider, all bright yellow as before; stigmatal stripe vague, less contrasting, often broken into spots which may be orange; just before the intersegmental membrane at the anterior end of each segment the subdorsal stripes are tinged more or less with orange. Venter gray-green (3D2) as before. Spiracles black. True legs and crochets black. The ground color contains very distinct darker, squarish black spots anteriorly at the front of each segment, as illustrated. Larvae "stem" the host, sitting quietly when not feeding. The last 1–3 fecal pellets are red-tinged. Time to leaving the host (prepupation), 8–9 days.

Prepupa. Formed away from the host, after several hours of wandering. Attached by the anal prolegs and a girdle around the thorax; usually vertically, head up. Length of prepupal period, 15–30 hr.

Pupa (Figs. 7–9). 20 × 5 mm. Initially colored like the prepupa, assuming its final coloration in 6 hr. Ground color ochre (5B3, "grayish orange") with numerous small



Figs. 1–9. *Tatochila distincta distincta* from Province of Jujuy, Argentina. 1. Egg. 2. Newly hatched larva showing primary tubercles and setae. 3. Mature larva, lateral view. 4. Same, dorsal view. 5. Frontal view of mature larval head capsule. 6. Mature larva, lateral view of seventh segment. 7. Pupa, dorsal view. 8. Pupa, lateral view. 9. Pupa, ventral view.

black tubercles corresponding to their larval positions, inconspicuous; head and appendage-cases darker ochre (5C4, "golden blonde") varying to slate green (25D5, "greyish green") with no to considerable black filling between the veins on the wing-cases. Dorsal and subdorsal lines present, yellow, weakly contrasting in life; a paler yellow shade below the spiracles; tongue-case long, nearly reaching the genital area. Attached head-up. Supraocular and frontal prominences moderate, about as in *T. xanthodice*; supraspiraculars very faintly if at all indicated; the mid-dorsal line moderately carinate on the thorax, slightly ridged on the abdomen but bearing no prominences. Pigment sequence as usual (eyes, wings, body; in females the white wing-color turns to yellow); meconium red (10B8, "currant"); time to hatch, 12–18 days.

DISCUSSION

As noted previously (Shapiro, 1979), the early stages of the *Tatochila sterodice* Stgr. species-group and those of *T. xanthodice* are very similar and support a close relationship between them. There are no great surprises in the early stages of *T. distincta distincta,* which show resemblances to both. The larva throughout its development retains the yellow mid-dorsal line, which is usually lost in *xanthodice.* The color scheme of the pupa is rather more like the *sterodice* group; the prominences are very similar to those of sympatric *macrodice,* and the tongue-case is the longest yet seen in *Tatochila.* On the basis of the early stages alone one would have no basis to assign this species to one species-group or the other; it appears that the morphology of *Tatochila* immatures is very conservative.

The wild host plant of this little-known species remains undiscovered, but it is surely a Crucifer feeder. Eggs were also obtained from the Peruvian subspecies, *T. d. fieldi* Herrera, on Crucifers but were subsequently lost. Members of the two species-groups not yet reared (the *orthodice* Weymer and *theodice* Bdv. groups; the former is heterogeneous and may be further subdivided) will not lay on Crucifiers in captivity (an association with Valerianaceae is suspected in some cases). Of the *Tatochila* karyotyped by de Lesse (1967), all the Crucifer feeders (*autodice* Hbn. of the *autodice* group and *vanvolxemii* Capr., *arctodice* Stgr., and nominate *sterodice,* all of the *sterodice* group) had n = 28 while three non-Crucifer feeders (*sagittata* Roeb. and either *orthodice* or *stigmadice* Stgr. of the *orthodice* group, plus *theodice*) had n = 27 and a fourth (either *stigmadice* or *orthodice*; the two were inadvertently confounded) had n = 28. These findings seem to strengthen the apparent division of the genus into at least two putative subgenera.

Tatochila distincta distincta occurs in the seasonally arid *puna* in a very different habitat from the *påramo*-dwelling north-Andean *xanthodice,* but shares with it a hilltopping epigamic strategy. In Salta and Jujuy males tend to fly 2–8 m downwind from the summit, rarely crossing it and usually remaining below the area patrolled by male *T. s. macrodice,* although interactions are not uncommon as both species circle between the summit area and the base of the mountain. *T. d. fieldi* may behave similarly; males believed to be this species, but never captured for certain identification, behave in this manner near Abra Málaga, Cusco. (Females have been collected down the canyon from the hilltopping site.) In Jujuy *T. d. distincta* co-occurs on or near summits with *Hypsochila wagenknechti sulfurodice* Ureta and *Phulia* "*nym-*

phula" Blanch. as well as *T. s. macrodice,* along with various other butterflies of which the most conspicuous is the nymphalid, *Yramea sobrina* Weym. It should be plain that hilltopping behavior has arisen many times, even within the Pierini, and that it is not useful in phylogenetic inference.

ACKNOWLEDGMENTS

Collections were made through the kindness of the staff of the Institute do Biología de la Altura, Universidad Nacional de Jujuy, Dr. Jose Scaro, Director, and with the special help of Lic. Estela Neder de Roman and Lic. Martha Arce de Hamity. This work was funded by the National Science Foundation under grant BSR-8306922 (Systematic Biology Program). The illustrations are by Karen English-Loeb.

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Received July 29, 1985; accepted October 25, 1985.

Note added in proof. On 23 January 1986 two female *T. distincta* were followed for about 30 min each at Tres Cruces and seven ovipositions were seen: four on *Astragalus garbancillo* Cav. and three on *A. micranthellus* Wedd. (Leguminosae) (determinations by R. Barneby, New York Botanic Garden). These are the first field host records of *T. distincta* and the first of any *Tatochila* (or indeed any Pierine) on a Legume. Both *Astragalus* are also hosts of *Colias blameyi* Jorg. at Tres Cruces; *A. garbancillo* is strongly ascending while *A. micranthellus* in low and tufted. The fact that *T. distincta* oviposits freely and develops to maturity on Crucifers in captivity suggests that Crucifer-feeding is primitive and *Astragalus*-feeding a derivative condition in *Tatochila.* I thank Mr. Robert Eisele for field companionship on the 1986 trip.

J. New York Entomol. Soc. 94(4):531–535, 1986

THE LIFE HISTORY OF *HYPSOCHILA WAGENKNECHTI WAGENKNECHTI,* A SCARCE BUTTERFLY FROM THE ANDES OF TEMPERATE CHILE (LEPIDOPTERA: PIERIDAE)

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Abstract.—Hypsochila wagenknechti wagenknechti from Chile is pivotal in the phylogenetic interpretation of the Andean Pierini because the adult appears to present a mixture of *Tatochila*- and *Phulia*-like characters. Its egg, larva, pupa, and aspects of its behavior and ecology are here described. Morphologically, the early stages are more like *Tatochila* than *Phulia,* but show some approach to the aberrant features of *Phulia* and *Pierphulia* in that the larva fails to eat its eggshell, is sluggish and rests on a silken mat, and the pupa is more rounded than any *Tatochila* yet described. The species is a Crucifer feeder, like *Phulia* and three of the five species-groups of *Tatochila,* but is unique among known Pierini of the region in laying small clutches of eggs.

This is the sixth in a series of papers describing the life histories of the Pierini of the Andean region. Of the nine endemic genera, previous treatments have covered *Reliquia* Ackery (Shapiro, 1978a), three species-groups of *Tatochila* Butler (Shapiro, 1978b, 1979, 1986a) and *Pierphulia* Field (Shapiro and Courtney, 1986), and papers are in preparation covering *Phulia* Herrich-Schaeffer, *Infraphulia* Field, and *Theochila* Field.

The genus *Hypsochila* Ureta is critical to the phylogenetic interpretation of the Andean Pierini, which have been taken as a monophyletic group by all previous workers (Field, 1958; Herrera and Field, 1959; Field and Herrera, 1977) except possibly Ureta (1963) who considered the lack of tibial spurs in the *Phulia* series of genera a subfamilial character. As noted by Field (1958) and Field and Herrera (1977), the combinations of characters found in the Andean genera are wildly discordant and make a phylogenetic analysis extremely difficult if not impossible. *Hypsochila* is at the center of most of these discordances. Thus, it groups with *Tatochila* and *Phulia* in uncus shape, with *Phulia, Piercolias* Stgr. and the Asiatic *Baltia* Moore in aedeagus, with *Phulia, Piercolias,* and *Baltia* in tibial spurs, with nothing in claws, paronychia, and pulvilli, and with *Theochila, Tatochila,* and *Piercolias* in venation. In habitus it closely resembles the *sterodice* Stgr., *xanthodice* Lucas, and *autodice* Hbn. species-groups of *Tatochila,* especially the first, and in genital morphology overall it is quite *Tatochila*-like. It is now evident that *Phulia, Infraphulia,* and *Pierphulia* at least share a bizarre set of morphological and behavioral specializations including very slow production of very large eggs, skipper-like larvae with sclerotized cervical shields living in individual silken nests, and rounded skipper- or moth-like pupae (Shapiro and Courtney, 1986; Shapiro, 1986b). It is also evident that at the enzyme biochemistry level, these genera cluster phenetically very far from *Tatochila,* seriously questioning the hypothesis of monophyly (Geiger and Shapiro, unpublished). Thus it is especially desirable to learn as much as possible about the early stages and biochemistry of the potentially intermediate *Hypsochila.*

Hypsochila ranges from southern Ecuador (G. Lamas, unpubl.) to Tierra del Fuego, at very high elevations in the central Andes to sea level in the far south. Nearly all of the named entities are very rare in collections, and the systematics of the genus (Field and Herrera, 1977) is in an unsatisfactory state because the characters used to distinguish species are weak and the ranges are very poorly known. The best-known *Hypsochila* is the nominate subspecies of *H. wagenknechti* Ureta, primarily because one can drive to its habitat in several Andean passes not far from Santiago, Chile. Even so, its life history has remained unknown until now. Its behavioral ecology is being described quantitatively (Courtney and Shapiro, 1986); qualitative observations bearing on its evolutionary relationships will be presented along with the descriptions of its immature stages, below. These descriptions are based on eggs and larvae collected from the field and eggs from captive females, all from the vicinity of Farellones and La Parva in the Cordón del Cepo, Province of Santiago, 2,500–3,500 m in January and February 1984. Most of these were reared in the field under uncontrolled (ambient) conditions, but those which had not metamorphosed were transferred at the end of the study to Davis, California where they completed larval development at 10L:14D, 23.9°/12.8°C. Preserved early stages are being retained at Davis at this time for comparative studies of chaetotaxy and development. Color descriptions were prepared from life, from preserved (but fresh) material, and from photographs taken in the field. Those in parentheses refer to the system of Kornerup and Wanscher (1978).

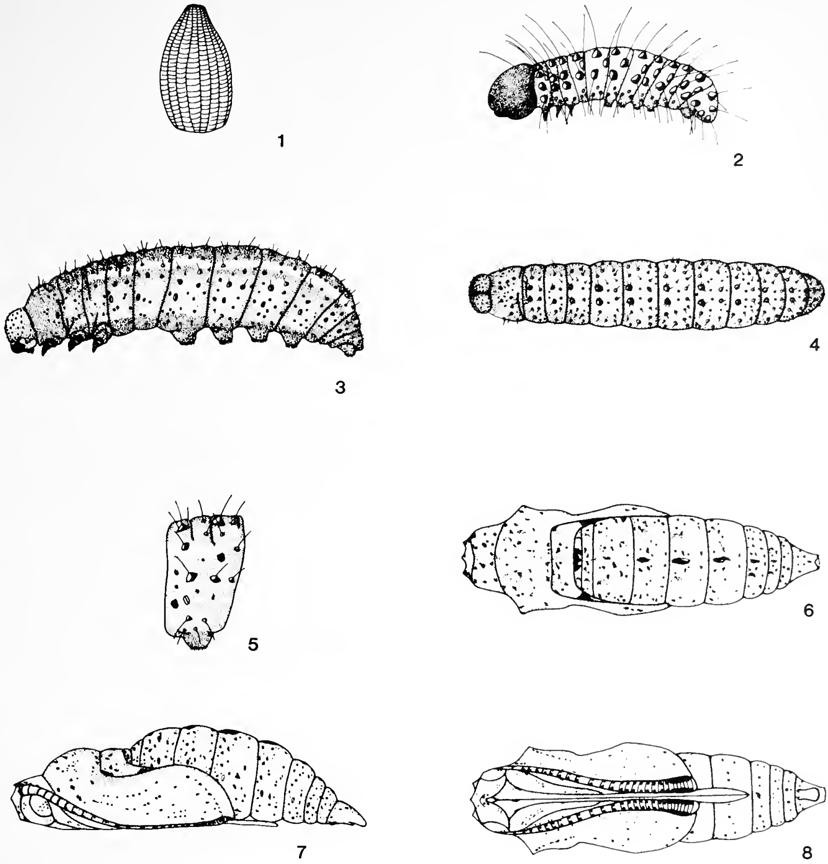
DESCRIPTIONS

Egg (Fig. 1). Erect, fusiform, 0.9 × 0.35 mm, the chorion sculptured as figured, with about 15 vertical and 30 horizontal ribs, the vertical ribs forming a vaguely beaded corona encircling the micropylar region. Laid on foliage of *Cardamine nivalis* (usually in small clutches) or *Lepidium suffruticosum* (usually singly) (both Cruciferae). Light orange-yellow to orange ("reddish orange," 7A7) when laid, turning slate gray 12 h before hatch. The larva eats a hole in the chorion below the apex, but consumes no more of the eggshell—in this regard differing from *Tatochila* and most Pierini, but resembling *Phulia* and its relatives. Time to hatch, 6 days.

Larva: First instar (Fig. 2). At hatch 1.0 mm at rest. Body buff gray ("pale orange," 5A3) with head dark brownish-black; body becoming gray-green ("grayish green," 26C3) after feeding; with a faint paler pattern of a dorsal and a pair of subdorsal lines, paler below the spiracles. Tubercles few, very large, bearing glandular hairs, black. Excavates pits in leaves and buds. Duration of instar, 2 days.

Second instar. After molt 1.9 mm long. Similar, the pattern more distinct, the tubercles proportionally smaller. Head vaguely mottled with yellowish, ocelli black. True legs brown-black. Length of instar, 3 days.

Third instar. After molt 2.8 mm long. Similar but darker slate gray ("greenish gray," 26C2), the dorsal stripe faint, subdorsals strong and contrasting, a more or less distinct



Figs. 1–8. *Hypsochila wagenknechti wagenknechti* from the Cordón del Cepo, Chile. 1. Egg. 2. Newly hatched larva showing primary tubercles and setae. 3. Mature larva, lateral view. 4. Mature larva, dorsal view. 5. Mature larva, lateral view of seventh segment. 6. Pupa, dorsal view. 7. Pupa, lateral view. 8. Pupa, ventral view.

yellow line through the spiracles, the body paler bluish-gray below; tubercles very distinct, black, bearing dark hairs. Length of instar, 3 days.

Fourth instar. After molt 5.0 mm. Similar to the previous instar. Some individuals show a distinct bright orange-red ("vermilion" = "cinnabar," 9A8) tinge in the subdorsal and stigmatal lines, and a vague orange tint in the light yellow-brown mottling on the head capsule. Time to molt, 4 days.

Fifth instar (Figs. 3–5). Initial length 14 mm, reaching 20 mm prior to prepupation. Head dark brownish gray mottled with orange-tinted yellow; ocelli black. Body striped lengthwise as follows: a single mid-dorsal line, yellow, usually very faint and commonly entirely absent, surrounded by a broad stripe of slate gray ("medium gray," 27E1) varying to purplish gray ("grayish magenta," 14E3), defined outwardly by a sharply contrasting yellow subdorsal line containing two distinct orange ("fire red," 7A8) spots in each segment; below this again slate to purplish gray, fading into brownish gray (4D2) below the spiracles, the transition area incorporating a series of brilliant red ("cinnabar" = "vermilion," 9A8) spots, one anterior and one posterior to each spiracle, generally strongly contrasting, in a few individuals contained within a diffuse yellow line; venter and prolegs brownish gray (4D2), faintly mottled with black; true legs gray with black mottling. Tubercles large, of three sizes, strongly contrasting, bearing short, stiff, dark hairs. The larva is sluggish, alternating between basking on the plant at low temperatures and concealing itself in the shade in the heat of the afternoon. It makes a silk platform, similar to a molting platform, on which it rests inside the plant, or on the sides of its container. Length of instar, 5–6 days. Final 1–3 fecal pellets pink.

Prepupa. Variously disposed, vertical (head up) or horizontal on the container lid, attached by a girdle of silk around the thorax and by the anal prolegs, on a silken platform which in containers may be a reworking of the last larval one, but in nature is made elsewhere after a period of several hours' wandering. Color as in the last instar, the markings becoming less contrasting. Time to pupation 36 hr.

Pupa (Figs. 6–8). Length 16 mm; width at girdle 4.25 mm. Attached as in the prepupa. Front of head and all appendage-cases, including wings, olivaceous brown ("oak brown," 5D6), the antennae strongly black-dotted as shown; top of head creamy white; dorsum of prothorax grayish-white mottled with brown except on the midline; mesothorax similar, the ground color orange-white (5A2), the keel creamy white; metathorax and abdomen gray brown (5D3, "nougat"), carinate, each segment bearing a black line anteriorly on its keel; on either side of the keels a row of large, raised, white tubercles, strongly contrasting; a faint whitish spiracular line; entire dorsum and ventral abdomen with many black tubercles; cremaster gray. Tongue-case moderate, its tip brownish. Frontal and supraocular prominences moderate, wing-bases markedly angular, but no trace of flaring supraspiracular prominences on the abdomen, and the thoracic keel is less developed than in *Tatochila,* though strongly contrasting. Overall, the pupa resembles a more-rounded-than-usual, small *Tatochila.* Like *T. autodice* and *T. blanchardii,* it appears to be an effective bird-dropping mimic, much like the Holarctic *Pieris* (*Pontia*) *beckerii* Edwards. Eyes, wings, and body pigmented in that order, white appearing in the wings 30 h and black 16 h before eclosion. This species has a facultative pupal diapause, which under 10L:14D, 21.1°/4.4°C terminated spontaneously in 4 months. We have not reared it directly. Meconium reddish pink.

DISCUSSION

The early stages of *Hypsochila w. wagenknechti,* though superficially fairly similar to *Tatochila,* offer some tantalizing resemblances to the *Phulia* group as well. Specifically: the larva fails to eat its eggshell; it is more sluggish than *Tatochila* and rests on a silken mat when not feeding; and the pupa has lost its supraspiracular prominences and reduced most of the others, including the thoracic keel. *Hypsochila* also has some unique attributes among the Andean Pierini reared thus far; it lays its eggs in small batches (but the larvae feed separately), and it has enlarged and very conspicuous larval tubercles. The suggestion of a corona around the micropyle of the egg is reminiscent of *Phulia* (but not of *Pierphulia*). The loss of the dorsal yellow line in the last instar is very reminiscent of *Tatochila xanthodice* (but not *T. distincta* of the same species group), with which Herrera and Field linked *Hypsochila* in genital morphology. The brilliant red spotting in the last two instars is reminiscent of some *Tatochila* but is a different color, and is unaccompanied by a matching collar.

The chaetotaxy of the Pieridae offers clear opportunities for clarifying phylogenetic relationships, but will require much more study before secure homologies are established and transformation series identified. It may ultimately prove of particular value in ascertaining the phylogenetic position of this enigmatic genus.

ACKNOWLEDGMENTS

Collections were made with the help of Dra. Mary T. Kalin Arroyo, Facultad de Ciencias, Universidad de Chile, whose gracious assistance we are pleased to acknowledge. This work was supported by the National Science Foundation under grant BSR-8306922 to A.M.S. (Systematic Biology Program). The illustrations are by Karen English-Loeb.

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Received July 29, 1985; accepted October 25, 1985.

J. New York Entomol. Soc. 94(4):536–541, 1986

THE LIFE HISTORY OF *PIERPHULIA ROSEA ANNAMARIEA*, AN UNUSUAL BUTTERFLY FROM THE PERUVIAN *ALTIPLANO* (LEPIDOPTERA: PIERIDAE)

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Abstract.—Pierphulia rosea annamariea is a very small pierine from the Peruvian highlands, whose entire life history is highly aberrant. The egg, larva, and pupa and various aspects of the behavior and ecology of immatures and adults are described. The larva, a Crucifer feeder, is skipper-like in appearance and habits and lives in an individual silken nest within rosettes of the host. The pupa is rounded and is formed in a loose cocoon. Adults lay very few, very large eggs but may live more than three weeks. Growth is exceptionally slow, requiring as much as half again longer from egg to adult as pierines twice the size, reared under the same conditions.

This is the fourth in a series of papers describing the preparatory stages of the Pierini of the Andean region. This tribe has undergone an extraordinary adaptive radiation in the Andes, with nine endemic genera and about 45 species in non-tropical or high-altitude tropical habitats, from northeastern Colombia to Tierra del Fuego. Previous treatments have appeared of *Reliquia santamarta* Ackery (Shapiro, 1978a), *Tatochila xanthodice* Lucas (Shapiro, 1978b), and the *sterodice* Stgr. and *autodice* Hbn. species-groups of *Tatochila,* comprising six entities (Shapiro, 1979).

The genus *Pierphulia* Field, formerly included in *Piercolias* Stgr., contains three species known from 3,000 to 5,000 m in the central Andes (Peru, Bolivia, and far northern Chile). At the time of the revision by Field and Herrera (1977), the only "natural history" available for any *Piercolias* was a vague, general habitat description for two species, and the life histories of all were unknown. Adult *Pierphulia* resemble miniature versions of *Piercolias*; they vie with the related genus *Infraphulia* Field as the smallest Pieridae in the world, with forewings 11–15 mm long. Like other small Andean Pierini, they show reduced venation (R_{4+5} anastomosed with R_3).

Pierphulia rosea annamariea Field and Herrera, 1977 is locally common in the Aguadas Blancas Reserve, Department of Arequipa, Peru (ca. 16°30′S), where Shapiro (1985) studied its behavior and ecology in 1983. In July 1984 several females were collected there and transported to Davis, California where oviposition was obtained. Larvae were reared in plastic Petri dishes (14 × 2.5 cm) as described below, in a growth chamber under 10L:14D, 23.9°/12.8°C. Culture is difficult, as discussed below. Preserved early stages are being retained at Davis at this time for comparative studies of chaetotaxy and development. Color descriptions were prepared from life. Those in parentheses refer to the system of Kornerup and Wanscher (1978).

DESCRIPTIONS

Egg (Fig. 1). Typically pierine in form; erect, milk-bottle-shaped, 1.20 × 0.33 mm, the chorion sculptured as figured, with about 17 vertical and 45 horizontal ribs. Laid singly out of sight on the under surfaces of leaves within small Cruciferous rosettes. Light orange ("reddish orange," 7A8) when laid, turning slate gray 12 h before hatch. The larva exits by the upper part of the egg, usually below the apex, but does not consume any more of the chorion than is necessary for this purpose; it thus leaves a superficially intact "eggshell," unlike most Pierini. Time to hatch, 6–7 days.

Larva: First instar (Fig. 2). At hatch 1.45 mm at rest. Buff gray ("pale orange," 5A3) with head black and apparently unpatterned; body becoming blue-green ("grayish green," 26B4) after feeding. There is a darker, more heavily sclerotized "cervical shield" on the prothorax dorsally, which is more conspicuous in preserved specimens than in life. Body with numerous small black tubercles bearing pale hairs. The larva excavates pits in soft tissue of any part of the plant, and constructs a very rudimentary silken mat on which it sits. Length of instar, 4 days.

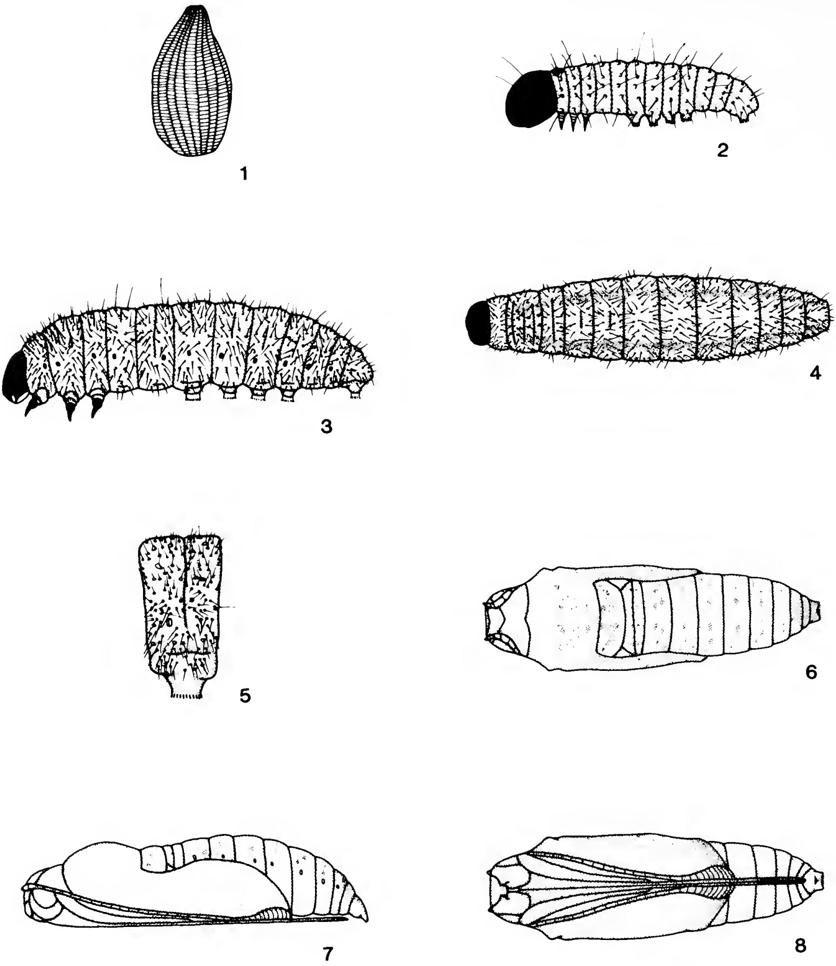
Second instar. After molt 3.2 mm long. Gray-green ("grayish green," 26C3) with an extremely faint pattern consisting of yellowish dorsal and subdorsal lines. Head and cervical shield brownish-black, vaguely lighter mottled. In this instar the larva constructs a loose silken shelter among the leaves near the apex of the rosette, within which it feeds, defecates, and molts. Length of instar, 4 days.

Third instar. After molt 5.1 mm. Similar but darker slate gray ("greenish gray," 26C2) sometimes with a vague purplish tinge, varying to blackish; the pattern only weakly contrasting, the cervical shield less distinct especially in darker individuals. Constructs a new nest after molting. Length of instar, 6 days.

Fourth instar. After molt 8.9 mm. As before, the pattern faint and most conspicuous in the darkest specimens (which are almost black). Again constructs a new nest after the molt. Length of instar, 8 days.

Fifth instar (Figs. 3–5). Initially 12 mm long, reaching 18 mm at maturity. Head dark purplish brown ("violet brown," 10E5) vaguely lighter mottled; mouthparts lighter gray brown ("brownish orange," 7C3). Body varying from purplish brown ("violet brown," 10E5) to brownish-black ("violet brown," 10F4) with an extremely faint middorsal line; slightly more contrasting but ill-defined subdorsal lines; a darker shade between the subdorsal and the spiracular area, which is greenish gray (1C2), occasionally with a vague darker line running through it at the level of the spiracles. Venter greenish gray (1C2) to light purplish brown ("violet brown," 11E4). True legs black, prolegs purplish brown externally and greenish gray on inner surface; crochets black. Cervical shield not contrasting. Body with numerous black tubercles of three sizes, more or less conical, bearing short gray simple hairs. Length of instar 10 days. The larva occasionally forages outside its nest in this instar. The last 1–3 fecal pellets are pinkish.

Prepupa. Variously disposed, vertical (head up) or horizontal; attached in the usual pierid fashion by the anal prolegs and a silken girdle around the thorax and wing-cases; within a very flimsy, transparent, net-like cocoon of white silk, often incorporating plant material or debris, or within the last larval nest. Color purplish brown ("violet brown," 11E5) with all markings very obscure, the ventral side of the thorax paler. Time to pupation 30 hr.



Figs. 1–8. *Pierphulia rosea annamariea* from Department of Arequipa, Peru. 1. Egg. 2. Newly hatched larva showing primary tubercles and setae. 3. Mature larva, lateral view. 4. Mature larva, dorsal view. 5. Mature larva, lateral view of seventh segment. 6. Pupa, dorsal view. 7. Pupa, lateral view. 8. Pupa, ventral view.

Pupa (Figs. 6–8). Length 12.8 mm; width at girdle 3.3 mm. Head and all appendage-cases dark slate green ("dull green," 26E3); abdomen brownish lilac ("grayish ruby," 12C4); wings often with some dark filling between veins, scarcely contrasting. Pupa with numerous black tubercles disposed in rows, corresponding to those of the larva; spiracles black; cremaster light purplish brown. Tongue-case very long, reaching or surpassing the penultimate segment; dorsal midline very weakly carinate on the thorax, scarcely at all on the abdomen; no frontal and only weak supraocular prominences; no flaring supraspiracular prominences; "shoulders" at bases of wings moderately pronounced. The pupa "looks teneral" until the pharate adult develops, because its color scheme is very similar to that of many Andean pierine pupae immediately after the molt. It wriggles very actively if disturbed. Eyes, wings, and body receive adult pigment in that order, with white appearing in the wings 24 hr and black 12 hr before eclosion. Meconium pink (12A3). Time to eclosion, 15 days.

DISCUSSION

Hardly anything about the biology of *Pierphulia rosea annamariea* is typical of the Pierini, Andean or otherwise.

Despite their small size and delicate appearance, adults are very hardy. Wild-collected females lived for over three weeks in captivity if fed daily and refrigerated at 2°C each night, and laid eggs every day until they died. Those eggs are, relatively speaking, the largest known in the Pieridae (and rival certain hesperiids); they are as large as or larger than the eggs of *Pieris* (*sens. lat.*) or *Tatochila* species twice their adult size. Only 3–5 eggs are laid/day when the opportunity is present to oviposit daily. In the field oviposition is often impeded by bad weather, and eggs can be accumulated up to 10–12. Lifetime egg production may frequently rival shorter-lived species which mature more eggs faster.

Captive females require very specific conditions for oviposition, both as regards thermal and light tolerances and substrate. After much trial and error, we found that they will lay freely on small (2–5 cm diameter) rosettes of the common weedy Crucifer *Lepidium virginicum* L., which also is acceptable for full development. Larvae reared on watercress, *Rorippa nasturtium-aquaticum* Schinz. & Thell., or seedlings of black mustard, *Brassica nigra* (L.) Koch., failed to survive to the fourth instar. The roots of the rosettes were kept wrapped in wet paper. They, the butterflies, and dandelion flowers (*Taraxacum officinale* Wigg.) were placed either in 14 × 2.5 cm plastic Petri dishes or 10 × 10 × 6 cm opaque plastic refrigerator boxes, both lined with rough paper toweling and both with transparent mesh tops, at 24°C with relative humidity ca. 30% in diffused or indirect sunlight. We were very surprised to see many eggs laid in the dandelion flowers, deep among the rays. This was done only in the immediate presence of Crucifers, and the larvae would not feed on the flowers. When ovipositing, the female stands "on tiptoe" with wings fully spread in the thermoregulatory "dorsal basking" posture, and probes deeply by bending the long ovipositor under leaves below the body. One female seemingly became habituated to laying in dandelions; after her 8th day in captivity she would hardly ever lay elsewhere, and she often fed and oviposited at the same time. We have seen the same behavior, albeit less frequently, in other small Andean Pierini. Either the cues received by the ovipositor are purely textural, or *P. rosea* can detect Crucifer chemistry at a distance of 2 cm or so without direct contact, but clearly the chemistry alone is insufficient as an oviposition stimulus since virtually no eggs were ever laid on non-rosette Crucifers, including *Lepidium* tops in various phenophases. The only known host plant in the wild is a very minute pinnatifid rosette Crucifer tentatively identified as a species of *Descurainia.*

The larva is sluggish and secretive, living in an individual web within the rosette. This nest usually incorporates the terminal bud, and by the time the larva is mature all the tender young tissue around it has usually been consumed. A new nest is built after each molt, but often directly adjacent to the old one. A few larvae left the original host in later instars and migrated to another. Feeding occurs both by day and night in our rearing conditions, but in the wild may be inhibited at night by subfreezing cold. Growth is the slowest we have ever seen in any pierine; at 10L: 14D, 23.9°/12.8°C, *P. rosea annamariea* takes 20% longer to mature than sympatric *Tatochila sterodice macrodice* Stgr. (more than twice its size) reared alongside it. It also takes half again longer than non-diapause *Pieris occidentalis nelsoni* Edwards from subarctic Alaska (Shapiro, 1975a, b), which resembles many Arctic-Alpine organisms in showing very rapid growth under mild conditions. No evidence of diapause was obtained, nor does it seem to occur afield, where there are 3–4 generations/yr depending on altitude, spanning both wet and dry seasons. Much of the high-Andean pierid fauna is tied to the peat bogs (*Turberas altoandinas,* Shapiro, 1985) which remain wet through the dry season, so continuous breeding is possible.

When mature, about half the larvae left the host and wandered for several hours before spinning the cocoon. Others simply enlarged the last larval nest, being careful, however, to pupate in an area free of frass. At least two larvae which deserted their nests wandered within their Petri dishes and then returned to the nests to pupate. This was probably an artifact of confinement. After one teneral pupa was partially eaten by a mature larva, all fifth instars were placed in individual dishes. The mature larva appears bloated, with a very small head, and superficially resembles a large curculionid larva or a hesperiid. Commencing in the first instar, the larva when not feeding usually rests in a coiled, head-to-tail posture very similar to a hesperiid in its nest. This combines with the nest-making habit and the cervical shield to create a powerful impression of convergence with that family. The roundness of the pupa is also skipper-like. It carries to an extreme the tendency seen in *Tatochila* for the reduction of the pupal prominences—a tendency also seen in the coliadine genus *Nathalis* Bdv., also of apparent high-Andean origin, and also greatly reduced in size.

In short, *P. rosea annamariea* differs from all other Pierini described to date in the following life history characteristics: 1. Small daily production of very large eggs. 2. Failure of the first instar larva to eat the chorion. 3. Reduced and simplified larval pattern. 4. Individual larval silken nest. 5. Individual silken cocoon. 6. Very slow growth. 7. Rounded pupa lacking nearly all the usual prominences.

In addition to the morphological oddities of the adult (Field and Herrera, 1977), it also has atypical mate-rejection behavior which is probably related to its unusual thermoregulatory posture (Shapiro, 1985; Shapiro and Courtney, 1985). All of these oddities are probably highly derivative, and reflect an integrated adaptive syndrome related to life in the *altiplano* (Shapiro, 1986).

ACKNOWLEDGMENTS

Collections were made with the help of Margaret J. Stern and Gerardo Lamas M. and were funded by the National Science Foundation under grant BSR-8306922 to A.M.S. (Systematic Biology Program). The illustrations are by Karen English-Loeb.

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Received July 29, 1985; accepted October 25, 1985.

J. New York Entomol. Soc. 94(4):542–551, 1986

THE PLANT BUGS (HEMIPTERA: MIRIDAE) ASSOCIATED WITH *ADENOSTOMA* (ROSACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—The Miridae associated with chaparral shrubs in the genus *Adenostoma* were collected throughout 1983 at two sites in southern California. Six species were taken from *Adenostoma fasciculatum* H. & A., and two from *A. sparsifolium* Torr. Although both shrubs commonly occur together their mirid associates overlap minimally. Only the widespread *Rhinacloa forticornis* Reuter occurs on both.

This is the second in a series of studies of the Miridae associated with major chaparral shrubs of southern California. An earlier paper examined the associates of *Ceanothus crassifolius* Torr. (Pinto, 1982). This study considers the mirids of the two closely related species of *Adenostoma, A. fasciculatum* H. & A., commonly known as chamise, and *A. sparsifolium* Torr., or red shank.

Adenostoma fasciculatum is the dominant component of chamise chaparral, the most common form of chaparral in California. This shrub forms extensive stands especially on hot, dry, south and west facing slopes and ridges from Trinity and Shasta counties in northern California south to northern Baja California (Hanes, 1977). *Adenostoma sparsifolium* is more restricted, with a patchy distribution from southern San Luis Obispo County in California south to near El Rosario in Baja California Norte. Almost 90% of the sites with *A. sparsifolium* are coinhabited by *A. fasciculatum* (Marion, 1943).

Although the two *Adenostoma* species are considered closely related, their growth and flowering periods are distinct. *Adenostoma fasciculatum* is active primarily in winter and early spring; *A. sparsifolium* is active from spring to autumn. Hanes (1965) presented an ecological study of the two shrubs.

This study was based on collections of all instars of Miridae on *Adenostoma* spp. at two sites in southern California throughout 1983. At one site only *A. fasciculatum* occurred; at the second, both species occurred together.

Objectives of the study were to determine the species of Miridae occurring on the two shrubs, their relative abundance, their occurrence relative to host phenology, the degree of interspecific seasonal overlap, and the degree of faunal overlap. A determination of faunal overlap was of particular interest considering the close relationship and extensive sympatry, but phenological dissimilarity of the two hosts.

SITE DESCRIPTIONS AND METHODS

The two sites utilized were as follows:

Site I. 33°39′N, 117°13′W; 550 m elev. Only *Adenostoma fasciculatum* occurs. This locale is in the low, dry hills to the immediate west of Menifee Valley, an ill-defined area near the southern terminus of the San Jacinto Plains in SW Riverside

County. The vegetation is dominated by chaparral but has a distinct Coastal Sage Scrub influence. This site was described more fully in a previous paper (Pinto, 1982).

Collections of Miridae at Site I were confined to an area of ca. 600 m^2 on a west facing slope of moderate gradient. *Adenostoma fasciculatum* forms an almost continuous cover on this slope except for scattered individuals of *Salvia mellifera* Greene (Labiatae), *Eriogonum fasciculatum* Benth. (Polygonaceae), and *Ceanothus crassifolius* Torr. (Rhamnaceae). The opposite, east facing slope is dominated by *Salvia mellifera, S. apiana* Jeps., and *Eriogonum fasciculatum.*

Site II. 33°42′N, 116°46′W; 1,150 m elev; ca. 45 km E of Site I. Coinhabited by *Adenostoma fasciculatum* and *A. sparsifolium,* the dominant perennials at this site. Occurring on a west facing slope at the SW end of the San Jacinto Mts adjacent to State Hwy 74, ca. 2 mi W of Mountain Center, this site is more mesic than Site I and the chaparral vegetation is considerably more dense and diverse.

Samples of Miridae were taken in a relatively restricted area of ca. 1,000 m^2 where the two *Adenostoma* intermixed and occurred in about equal frequency. To the immediate east (upslope), *A. fasciculatum* dominated; to the west (downslope) *A. sparsifolium* dominated. *Arctostaphylos glauca* Lindl. (Ericaceae) is widely scattered throughout the area. Other less common perennials include *Cercocarpus betuloides* Nutt. ex T. & G., *Prunus ilicifolia* (Nutt.) Walp. (Rosaceae), *Ceanothus cuneatus* (Hook.) Nutt., *Ceanothus leucodermis* Greene (Rhamnaceae), *Quercus dumosa* Nutt. (Fagaceae), *Eriodictyon crassifolium* Benth. (Hydrophyllaceae), *Lonicera involucrata* (Richards) Banks (Caprifoliaceae), and *Garrya veatchii* Kell. (Garryaceae).

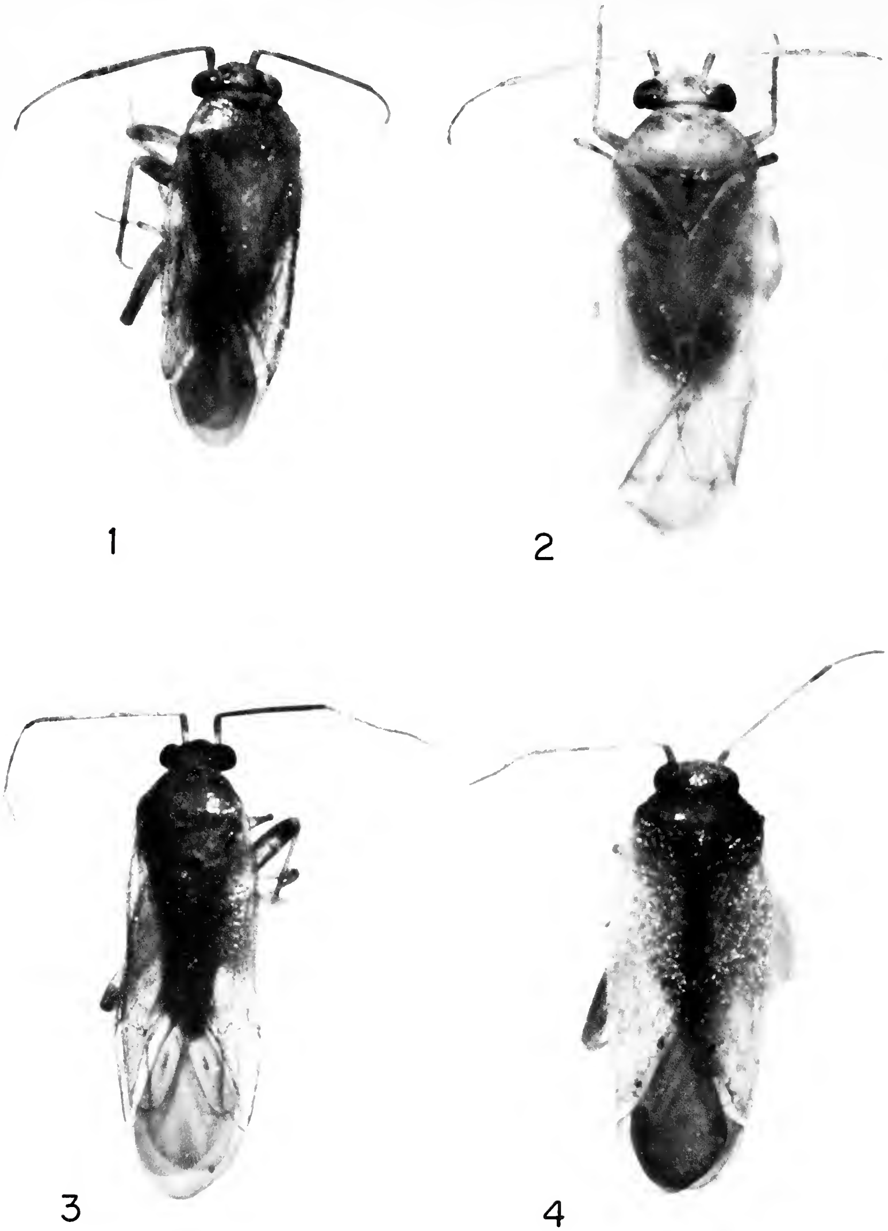
Ten mature shrubs of *A. fasciculatum* were sampled at Site I from 1 January to 15 December 1983. Except for an hiatus of two weeks in late summer, collections were taken approximately once a week with a mean of 7.4 da (range, 4–11) between samples. Ten shrubs each of *A. fasciculatum* and *A. sparsifolium* were sampled at Site II from 6 January to 12 December 1983. Collections were taken approximately once every two weeks with a mean of 12.2 da (range, 5–17) between samples. Several additional collections were made at two week intervals at Site I in 1985 from February–May. Early 1985 was much drier and warmer than the equivalent period of 1983, and the purpose of these collections was to compare seasonal distribution and abundance of one of the vernal species.

Collecting procedures closely followed those used in the study of *Ceanothus* Miridae (Pinto, 1982). Collections were made by beating hosts and allowing specimens to fall into a modified sweep net, 12 cm deep and 28 cm in diameter. Three positions at 1–1.5 m height were sampled on each shrub. Care was taken to sample plants that were not contacting other species. Specimens were quickly aspirated at each position and killed in cyanide after all plants were sampled. Most of the immatures were transferred to 70% alcohol. Adults were either point mounted or also placed in alcohol. All sampling was done between 1000–1400 hr.

Larvae and adults were easily associated by traits common to both. Rearings verified these associations.

Precipitation and average temperatures relative to mirid seasonal distribution are given for Site I (Fig. 7). Rainfall was recorded on site; temperatures were taken from U.S. Climatological Data for Sun City, CA, ca. 3.5 km from the collecting area.

Voucher specimens from this work are located in the collections of the Department



Figs. 1–4. Males of three species of Miridae occurring on *Adenostoma fasciculatum*. 1. *Microphylidea* sp. or near (dark form). 2. *Microphylidea* sp. or near (light form). 3. *Orthotylus fraternus*. 4. *Parthenicus picicollis*. Body length for specimens in Figures 1–4: 2.7, 3.5, 3.0, and 4.2 mm, respectively.

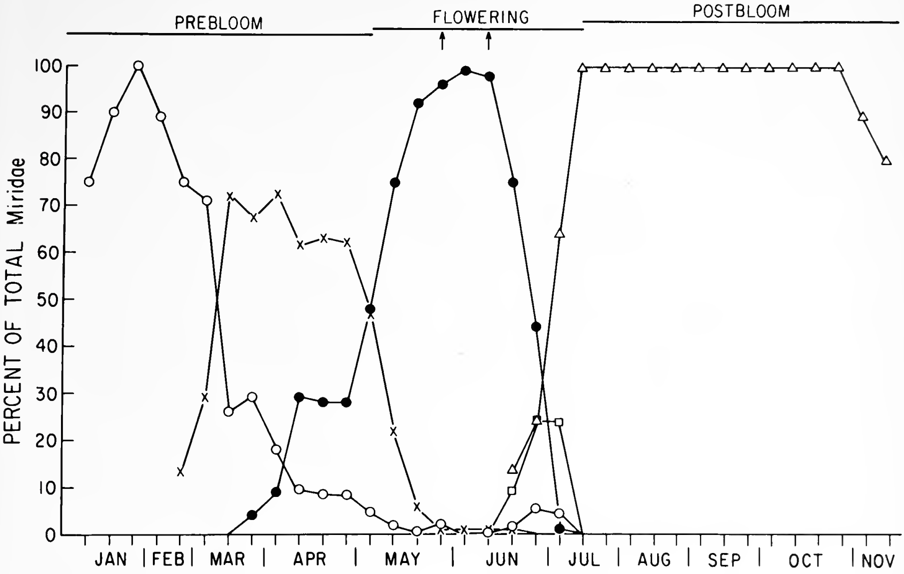


Fig. 5. Phenology of Miridae and *Adenostoma fasciculatum* at Site I (Menifee Valley, CA) during 1983. Adults and immatures combined for each species. ○ = *Phytocoris vau*; × = *Orthotylus fraternus*; ● = *Microphylidea* sp. or near; □ = *Rhinacloa forticornis*; △ = *Parthenicus picicollis. Phytocoris californicus* not included but considered in calculating percentages. Arrows at top delimit period of maximum flowering of *A. fasciculatum.*

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RESULTS

Adenostoma fasciculatum Associates

Six species of Miridae were found to develop on *A. fasciculatum.* These include two Mirinae, *Phytocoris californicus* Knight and *Phytocoris vau* Van Duzee; two Orthotylinae, *Orthotylus fraternus* (Fig. 3) Van Duzee, and *Parthenicus picicollis* Van Duzee (Fig. 4); and two Phylinae, *Microphylidea* sp. or near (Figs. 1, 2), and *Rhinacloa forticornis* Reuter.

Phytocoris californicus was uncommon. It was represented only by four larvae collected in winter and three adults taken in summer of 1983. It was found only at Site I and is not considered further.

The identification of *Microphylidea* sp. is tentative. Also, distinct light and dark forms of this species are grouped under this identification (Figs. 1, 2); only adults were distinguished (Fig. 6). Additional work is needed to determine if they represent distinct species.

Rhinacloa forticornis is a common species with numerous recorded plant associations (e.g., Knight, 1968). The other species (except *P. californicus*) are known only

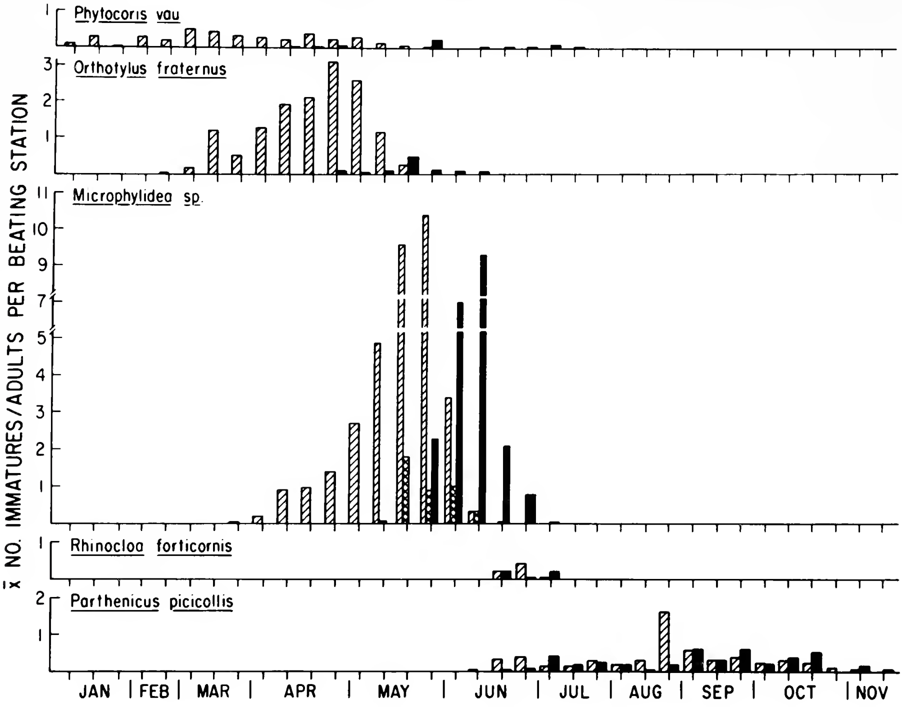

Fig. 6. Phenology and relative abundance of Miridae at Site I (Menifee Valley, CA) on *Adenostoma fasciculatum* during 1983. Bars with diagonal markings = immatures; solid bars = adults; for *Microphylidea* sp. bars with cross hatching = dark form adults, solid bars = light form adults. x̄ No. per beating station calculated by dividing total catch by 30 (10 plants, 3 stations per plant).

from chamise. *Parthenicus picicollis* and *Phytocoris vau* were previously recorded from this host (Van Duzee, 1916; Knight, 1968); the occurrence of *Orthotylus fraternus* and *Microphylidea* sp. on chamise are new records.

Sampling results for Site I are presented in Figures 5 and 6. Figure 5 gives the percentage of all stages of each species on *A. fasciculatum* relative to total number of Miridae per sampling day. Figure 6 considers the relative abundance of adults and larvae of each species. The mean number of individuals per beating station (total catch divided by 30) is given for each sampling day.

Mirids were collected from *A. fasciculatum* at Site I during all months of 1983 except December. No adults or mature larvae were collected until late spring, indicating that all species overwinter in the egg stage.

Each species except *Rhinacloa forticornis* was dominant at some time of the year (Fig. 5). However, only *Orthotylus fraternus* and *Microphylidea* sp. were abundant (Fig. 6). Both occurred immediately before and during flowering and closely followed the time of maximum rainfall (Figs. 5, 7).

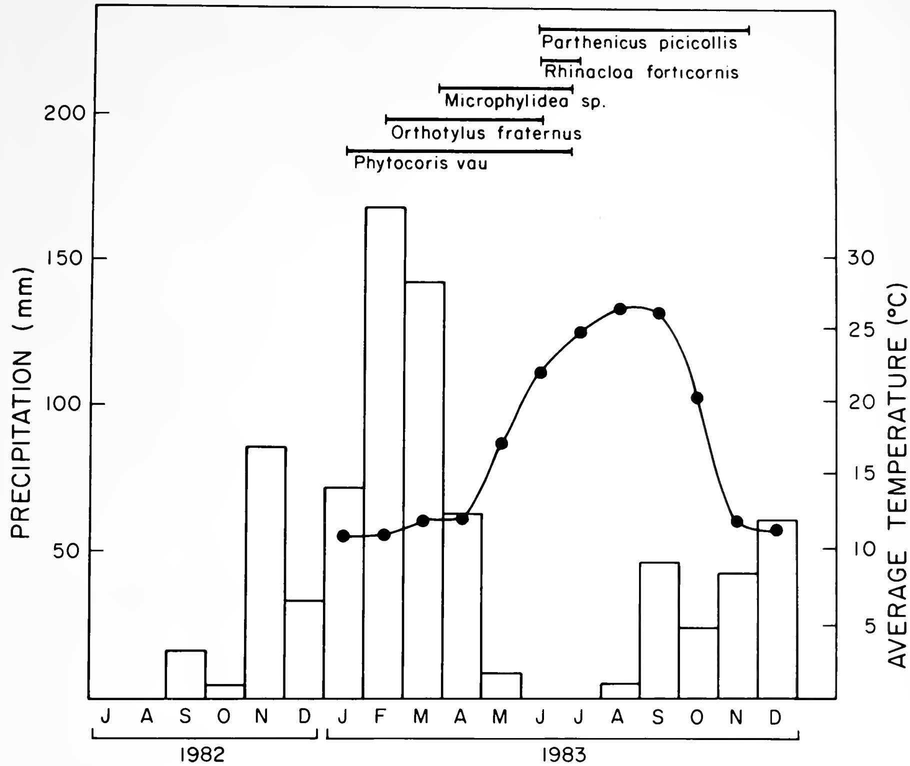

Fig. 7. Seasonal distribution of Miridae at Site I (Menifee Valley, CA) relative to monthly precipitation (bars) and average monthly temperature (connected dots) during the last half of 1982, and 1983.

Phytocoris vau, the first species to appear, occurred in low numbers but had the broadest seasonal range (mid-January–early July). Early instar larvae were collected in January, and adults were not taken until early April (Fig. 6). Only early instars (1–3) were present in January and February; fifth instars did not appear until late March. This suggests slow larval development and perhaps high levels of larval mortality during the winter.

Orthotylus fraternus (Fig. 3) was the second species collected; it occurred for approximately four months (February–June). That larvae were much more common than adults (Fig. 6) suggests high larval mortality (see below). This species was most abundant immediately before flowering of its host (Fig. 5).

Microphylidea sp. (Figs. 1, 2), the third species, was abundant both as larvae and adults. It was the most common species during peak bloom of *A. fasciculatum.* Larvae were first collected a month after the appearance of *O. fraternus,* and adults were active almost a month after the latter had waned. This asynchrony notwithstanding, the activity period of larvae and adults of both species overlapped broadly. The

Table 1. Comparison of seasonal distribution during 1983 of Miridae on *Adenostoma fasciculatum* at Menifee Valley (Site I) and near Mtn Center, CA (Site II).

	Site I		Site II	
Species	1st appearance of larvae	1st/last appearance of adults	1st appearance of larvae	1st/last appearance of adults
Phytocoris vau	Jan 16	Apr 10/Jul 14	May 19	Aug 18[2]
Orthotylus fraternus	Feb 20	Apr 26/Jun 14	Apr 19	May 19/Jun 30
Microphylidea sp. (dark form)	Mar 27	May 4/Jun 22	May 19	Jun 24/Jun 30
Microphylidea sp. (light form)	?[1]	May 22/Jul 6	?[1]	Jun 24/Jul 18
Parthenicus picicollis	Jun 14	Jul 18/Oct 31	May 3	Jun 22/Nov 22[3]
Rhinacloa forticornis	Jun 22	Jun 22/July 6	Jun 24	Jun 30/Sept 12

[1] Not distinguished from dark form larvae.
[2] Only a single female collected.
[3] One adult also collected in January.

disappearance of *Microphylidea* sp. coincided with the end of blooming. The dark form of this species was much less abundant and occurred somewhat earlier than the light form (Fig. 6).

Rhinacloa forticornis occurred in low numbers on *A. fasciculatum.* Adults and larvae were collected on three sampling dates in late June and early July, coinciding with the second half of the flowering period. As with *Microphylidea* sp., it disappeared at the end of flowering (Fig. 5). Considering that *R. forticornis* is known from numerous plants and that adults were not preceded by larvae (Fig. 6), we assume the species moved to chamise from other host(s), produced a single generation, and then migrated to other plants when flowering ceased.

Parthenicus picicollis was the only mirid on *A. fasciculatum* after flowering (Fig. 5). It occurs during the hottest and driest months (Fig. 7) when host growth has slowed or ceased entirely. Its period of activity was almost as broad as that of *Phytocoris vau,* occurring in relatively low numbers from mid-June to the end of November. Only late instar larvae and adults were collected in July. All stages of larvae and adults were taken on almost all sampling dates from August to mid-November (Fig. 6). This strongly suggests more than a single generation.

Collections on *A. fasciculatum* at Site II were similar. The same species occurred, and their sequence of occurrence and relative abundance were similar. As expected due to higher elevation, the earlier species were delayed at Site II (Table 1); the two summer species were not. *Rhinacloa forticornis* was collected at about the same time at both sites, and *P. picicollis* actually was taken first at Site II. *Phytocoris vau* was uncommon at Site II, known only from two larvae and one adult.

Adenostoma sparsifolium Associates

Only two species of Miridae were collected on *A. sparsifolium, Rhinacloa forticornis* and *Phytocoris adenostomae* Stonedahl. The latter, recently described species (Stonedahl, 1985) is known only from red shank.

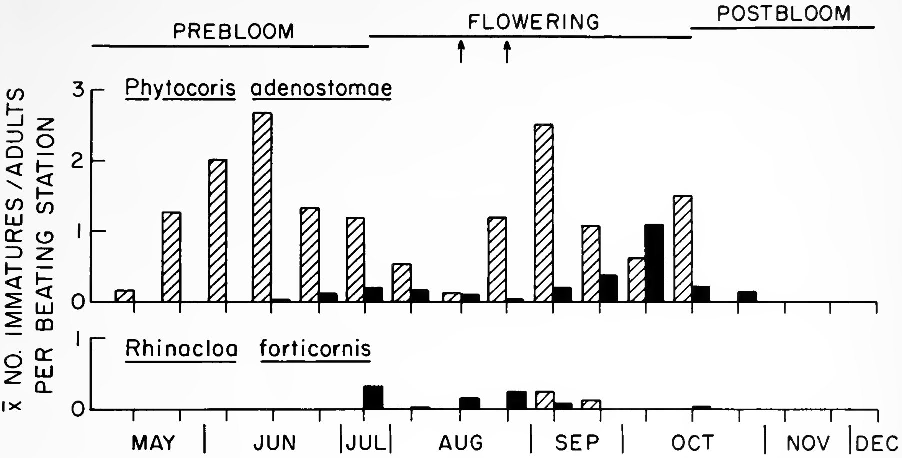

Fig. 8. Phenology and relative abundance of Miridae on *Adenostoma sparsifolium* at Site II (nr Mountain Center, CA) during 1983. Phenology of host plant indicated at top; arrows delimit period of maximum flowering. Bars with diagonal markings = immatures; solid bars = adults. x̄ No. per beating station calculated by dividing total catch by 30 (10 plants, 3 stations per plant).

Phytocoris adenostomae was abundant and active for about six months (mid-May–late November, Fig. 8). The seasonal bimodality of larval abundance and the presence of first and second instars as late as September suggest at least two generations. The activity period of this species straddled the flowering period of its host. It appeared almost two months before blooming began and waned in fall about one month after blooming ceased.

Rhinacloa forticornis adults and larvae were taken in small numbers on *A. sparsifolium.* All were collected during flowering (Fig. 8).

Feeding

All species except *R. forticornis* were observed feeding in the laboratory. *Phytocoris vau* (larvae and adults), *Orthotylus fraternus* (larvae), and *Microphylidea* sp. (larvae and adults) commonly fed on unopened flower buds and stems within the panicled inflorescences. Feeding on leaves was not observed. Adults and at least one larva of *Parthenicus picicollis* fed along the mid-vein of the linear leaves of *A. fasciculatum.* Flowers were not available to this species except at the beginning of its activity period. *Phytocoris adenostomae* fed at the tips of young stems and along the mid-vein of leaves of red shank. One adult also was observed feeding on a conspecific. It is unknown if this individual was killed or already dead when feeding began.

DISCUSSION

One interesting aspect of this study is the demonstration that the two *Adenostoma* harbor distinct species of Miridae. The presence of the widespread *Rhinacloa forticornis* on both is the only exception. Since the *Adenostoma* species are intermixed at Site II the lack of substantive faunal overlap is attributable to host specificity rather than geographic or habitat differences.

Important differences between the two hosts are their periods of seasonal growth and reproduction. According to Hanes (1965) growth in *A. fasciculatum* is initiated in January and decreases greatly in June. April and May are months of maximum growth. Flowering usually occurs from April to June. *Adenostoma sparsifolium* grows prolifically in May and June and continues at a relatively high level until late autumn. Flowering occurs primarily in August and September.

Mirid activity correlates well with host phenology. Four of the five species on *A. fasciculatum* occur during its growing season. *Parthenicus picicollis* is the only species active when the plant is quiescent. The two most abundant mirid species, *Orthotylus fraternus* and *Microphylidea* sp., occur immediately before and during flowering. Similarly, *Phytocoris adenostomae* occurs on *A. sparsifolium* from May to November, later than most of the mirids on chamise, but during the primary period of growth and reproduction of its host.

The occurrence of *Rhinacloa forticornis* on both species at Site II also correlates with host phenology. It occurs primarily in June on *A. fasciculatum* and from late July to October on *A. sparsifolium.* The occurrence of single adults on chamise in August and September (Table 1) probably represents strays from neighboring *A. sparsifolium.*

The absence of faunal overlap cannot be attributed solely to asynchrony of host growth and flowering because the two *Adenostoma* grow considerably in spring when mirids are active on both. For example, adults and larvae of *P. adenostomae* occur on *A. sparsifolium* in May and June when *A. fasciculatum* is still in bloom. Their absence from adjacent chamise indicates that it is unacceptable as a host.

Much of the data reported here on relative abundance and, perhaps, on breadth of seasonal range should be considered within the context of prevailing climatic conditions. For example, collections of *Orthotylus fraternus,* an early species, showed marked differences in seasonal distribution and abundance in 1983 and 1985. In 1983 larvae were present for more than two months before adults were taken in late April (Fig. 6). Also, mortality apparently was high between the larval and adult stage. In 1985, however, adults were first collected in early March, a month and a half earlier. They also were much more numerous (as many as 8.0 individuals per beating station in 1985, compared to a maximum of 0.5 in 1983).

Climatic conditions were dramatically different during the early months of these two years. Early 1983 was cool and wet with rainfall for February, March and April at Site I 127, 203, and 70 mm, respectively. Average precipitation for these months for locales near Site I are ca. 60, 50, and 25 mm, respectively. By contrast, 1985 was much warmer and quite dry. Only 31 mm of rain fell from February–May, considerably less than average. Since host phenology also differed during these two years the climatic effect on *O. fraternus* may be indirect. In any event, although abundance and seasonal distribution varied in this species, its sequence of appearance relative to others did not.

ACKNOWLEDGMENTS

The authors wish to thank the following for assistance in this study: Thomas Henry, Systematic Entomology Laboratory, USDA, for identification of Miridae; Andrew Sanders, U.C. Riverside

Herbarium, for plant identifications; and Max Badgley and Patricia Mote for preparation of Figures 1–4 and 5–8, respectively.

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Received September 17, 1985; accepted November 15, 1985.

J. New York Entomol. Soc. 94(4):552–558, 1986

A NEW SPECIES AND NEW SYNONYMY IN THE GENUS *TEPA* ROLSTON AND MCDONALD (HEMIPTERA: PENTATOMIDAE)

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Abstract.—*Tepa vanduzeei* is described as new from the western United States and Mexico; *Thyanta punctiventris* Van Duzee is placed in the synonymy of *Tepa rugulosa* (Say); and *Thyanta coloradensis* Bliven is placed in the synonymy of *Tepa jugosa* (Van Duzee). Lectotype and paralectotype designations are made for *Thyanta brevis* Van Duzee and *Thyanta punctiventris. Tepa jugosa* is reported from the United States for the first time. A key is provided for the identification of the 6 species of *Tepa.*

Rolston (1972) reviewed the small species of *Thyanta* Stål which occur in North America. This work included 8 species, of which *T. antiguensis* (Westwood) and *T. elegans* Malloch have been transferred to *Cyptocephala* Berg by Rolston and McDonald (1984). The remaining 6 species formed a homogeneous group distinct from *Thyanta,* and Rolston and McDonald (1984) described the genus *Tepa* to hold these species.

Tepa is New World in distribution and occurs mainly in Mexico and the western United States with one species also occurring in southern Florida and Curacao. *Tepa* belongs to the group of pentatomine genera which lacks a spine or tubercle at the base of the abdominal venter. A key to separate those genera that occur in the Western Hemisphere north of South America is provided by Rolston and McDonald (1984).

The type specimens for most of the species of *Tepa* have been examined recently, and several corrections to previous contributions are necessary. *Thyanta punctiventris* Van Duzee is placed in the synonymy of *Tepa rugulosa* (Say), *Thyanta coloradensis* Bliven is placed in the synonymy of *Tepa jugosa* (Van Duzee), and *Thyanta punctiventris* of authors (not Van Duzee) is described as a new species.

The following key is a modification of the one provided by Rolston (1972). Rolston (1972) also provided excellent figures for all the species of *Tepa.*

KEY TO SPECIES OF *TEPA*

1. Distance from mesial margin of ostiole to apex of ruga much greater than distance from apex of ruga to lateral margin of supporting sclerite 2

– Distance from mesial margin of ostiole to apex of ruga equal to or less than distance from apex of ruga to lateral margin of supporting sclerite 4

2(1). Ostiolar canal widening toward apex; lateral lobe of paramere bent strongly entad. (Baja California, southwestern United States) .... *T. jugosa* (Van Duzee)

– Ostiolar canal narrowing toward apex; lateral lobe of paramere bent weakly entad 3

3(2). Anterior lobe of paramere narrowed apically, lateral lobe of paramere usually bent weakly toward anterior lobe (see Rolston, 1972, fig. 42) (western United States, Mexico) .... *T. vanduzeei,* n. sp.

– Anterior lobe of paramere not narrowed apically, lateral lobe of paramere bent strongly toward anterior lobe (see Rolston, 1972, fig. 36) (Baja California, Curacao, Florida keys) . . . . *T. panda* (Van Duzee)

4(1). Lateral margins of head converging sinuously, nowhere parallel; ostiolar ruga nearly evanescent apically in profile; lateral lobe of paramere bent strongly entad (western United States) . . . . *T. brevis* (Van Duzee)

– Lateral margins of head subparallel for some distance between eyes and apex of head; ostiolar ruga truncate apically in profile; lateral lobe of paramere not bent strongly entad 5

5(4). Anterolateral margins of pronotum straight; proctiger with prominent mesial ridge for much of its length, strongly impressed on each side of ridge; rim of genital cup continuing onto ventral surface of pygophore as short, oblique, mesially convergent carinae (western United States) . . . . *T. yerma* (Rolston)

– Anterolateral margins of pronotum concave; proctiger bulbous near base; ventral surface of pygophore not carinate (western United States) . . . . *T. rugulosa* (Say)

Tepa brevis (Van Duzee)

Thyanta brevis Van Duzee, 1904:53, 56–57.
Tepa brevis: Rolston and McDonald, 1984:77, 80, fig. 44.

Van Duzee described *Thyanta brevis* in 1904 from 10 specimens collected at Grand Junction, Colorado. Although he placed "holotype" and "paratype" labels on the pins with the specimens, he did not actually make these designations in his original description. Strict adherence to the rules of nomenclature dictates that these specimens should be considered syntypes, and lectotype and paralectotype designations are required.

Of the original syntype series only one male and one female were located. The male specimen labeled "Gnd Junc Col. 7-28-00/ E P Van Duzee collector/ HOLOTYPE brevis" is here designated as the lectotype, and the female specimen labeled "Gnd Junc Col. 7-28-00/ E P Van Duzee collector/ PARATYPE brevis" is designated the paralectotype.

Tepa brevis can be recognized by the relatively short ostiolar rugae which are evanescent apically when viewed in profile. It also has the jugal margins nowhere parallel with the apex of the head narrowly rounded. *Tepa rugulosa* and *T. yerma* both have the ostiolar rugae relatively short, but in both of these species it is truncate apically when viewed in profile; also the lateral margins of the head are subparallel for some distance between the eyes and the apex. Specimens of *T. brevis* have been examined from Arizona, California, Colorado, Nevada, New Mexico, Texas, Utah, and the Mexican states of Baja California Norte, Chihuahua, Nuevo Leon, and Sonora.

Tepa jugosa (Van Duzee)

Thyanta jugosa Van Duzee, 1923:129.
Thyanta coloradensis Bliven, 1956:5–6, pl. 1, fig. 9. **NEW SYNONYMY.**
Tepa jugosa: Rolston and McDonald, 1984:77, 80, fig. 45.

Rolston (1972) noted that the description and illustration of *Thyanta coloradensis* Bliven agreed in all significant respects with the characters of *Tepa punctiventris,* but the type specimens of *Thyanta coloradensis* were not available for study at that time, and Bliven's description was inadequate for proper placement of the species. The holotype of *T. coloradensis* has now been examined, and it is a typical example of *Tepa jugosa.* The holotype of *T. jugosa* was also examined.

Tepa jugosa is probably the most easily recognizable species in the genus. The long ostiolar rugae which widen apically separates it from all other species in the genus. *Tepa jugosa* has previously been reported only from Baja California, Mexico. Specimens have been examined from the following U.S. localities: **Arizona:** *Cochise Co.,* Benson, 23 July 1907, CAS (♀); Douglas, F. H. Snow, SMEK (2♀♀). *Maricopa Co.,* Buckeye, 17 May 1932, E. D. Ball, UAT (♂), 7 June 1935, H. G. Johnston, TAMU (♂ ♀), 14 June 1935, H. G. Johnston, TAMU (♀), 11 May 1937, E. E. Russell, ASUT (♀); Litchfield Pk., 10 June 1948, M. H. Frost, Jr., UAT (♀); Phoenix, 6 May 1931, E. D. Ball, UAT (♀), 13 May 1937, ASU (♀). *Pima Co.,* Tucson, 24 July 1930, E. D. Ball, UAT (♂ ♀), 15 April 1933, Bryant, OSUC (♀), 2 Aug. to 14 Sept. 1935, J. R. de la Torre Bueno, SMEK (15♂♂ 20♀♀), 6 July 1958, G. D. Butler, at light, UAT (♀). *Pinal Co.,* Sacaton, 23 July 1931, E. D. Ball, UAT (♂), 2 Apr. 1932, E. D. Ball, UAT (2♂♂), 11 July 1947, R. E. Elbel, SMEK (♂). *Santa Cruz Co.,* Amado, 13 July 1958, G. D. Butler, UAT (♀). *Yuma Co.,* Yuma, 7 Apr. 1879, INHS (♂). **California:** *Riverside Co.,* Indio, 24 Apr. 1952, Bryant, CAS (2♂♂). *San Bernardino Co.,* Needles, 1–2 Jan. 1954, B. P. Bliven, CAS (3♀♀); San Bernardino, 17 Apr. 1879, INHS (♂). *San Diego Co.,* 25 June 1913, E. P. Van Duzee, CAS (♂). **Texas:** *Brewster Co.,* Terlingua, Sept. 1939, S. E. Jones, ISU (♂). *Hudspeth Co.,* Fort Hancock, 13 July 1938, R. I. Sailer, SMEK (♂ ♀). This is the first report of its occurrence in the United States.

Tepa rugulosa (Say)

Pentatoma rugulosa Say, 1832:319.
Thyanta rugulosa: Uhler, 1872:399.
Thyanta punctiventris Van Duzee, 1904:53, 55–56. **NEW SYNONYMY.**
Tepa rugulosa: Rolston and McDonald, 1984:77, 80, fig. 42.

The type specimen of *Pentatoma rugulosa* is no longer in existence; however, the original description is adequate to fix the species. Say (1832) stated that *P. rugulosa* has the "thorax much contracted before; lateral edge rather concave than rectilinear: tergum black at base, the three ultimate segments and the margin green." *Tepa rugulosa* is the only species in the genus with both the anterolateral margin of the pronotum distinctly concave and the tergum black as in the above description.

Van Duzee (1904) stated that his new species *Thyanta punctiventris* may only be a color variety of *T. rugulosa.* Several species of *Tepa* and the closely related genus *Thyanta* are now known to have several color forms. The different color forms are determined by environmental factors and have no geographical significance (McPherson, 1977, 1978; Ruckes, 1957). The type specimens of *Thyanta punctiventris* have been examined, and structurally they are typical specimens of *Tepa rugulosa.*

Once again, Van Duzee did not officially designate a holotype or paratypes in his original description of *Thyanta punctiventris.* Only 6 of the original 12 syntype specimens were located. The male specimen labeled "Willist'n N. D. Jun. 8–9 Wickham/ HOLOTYPE punctiventris" is here designated as the lectotype. The remaining 5 specimens are designated as paralectotypes. They have the following locality data:

"Willist'n N. D. Jun. 8–9 Wickham/ PARATYPE punctiventris" (♀); "Colo 1163/ Det. Uhler/ PARATYPE punctiventris" (♀); "Salt Lake, 14-6-98, Ut/ Heidemann Collector/ PARATYPE punctiventris/ E P Van Duzee Collection" (♀); "Gnd Junc Col. 7-28-00/ E P Van Duzee Collector/ PARATYPE punctiventris/ E P Van Duzee Collection/ Thyanta punctiventris Van D., Det. V. D." (♀); and "Gnd Junc Col. 7-27-00/ E P Van Duzee Collector/ PARATYPE punctiventris/ E P Van Duzee Collection" (? — abdomen missing).

Specimens of *T. rugulosa* have been examined from British Columbia, Canada, and from the following states: Arizona, California, Colorado, Idaho, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming.

Tepa vanduzeei, new species

Thyanta punctiventris: Hart, 1919:217 (misidentification).
T. punctiventris: Torre-Bueno, 1939:232 (misidentification).
T. punctiventris: Rolston, 1972:283, figs. 37–42 (misidentification).
Tepa punctiventris: Rolston and McDonald, 1984:78, 80, fig. 47 (misidentification).

Description. Dorsum of typical form medium green, often with scutellum, head, connexivum, and anterior third of pronotum pale; punctation dense, shallow, rugulose, usually less dense on hemelytra; punctures green. Ventral surface pale green to yellow, each posterior abdominal angle black; punctures less dense than on dorsum, concolorous with surface. Antennae pale to medium green or brown, apical two segments usually darker. Legs pale to medium green, apices of tibiae often becoming fuscous. Dorsum of brown form light tan to brown, often tylus and area of head between ocelli darker, usually with pale mesial line on scutellum, this line often extending onto pronotum. Dorsal punctation concolorous with surface except on hemelytra, scutellum, and anterior and posterior margins of connexival segments, fuscous. Ventral surface pale brown with fuscous punctures; a series of black postspiracular spots usually present; anterior and posterior abdominal angles black. Antennae pale to medium brown, apical two segments usually fuscous. Legs pale to medium brown with numerous fuscous spots scattered over surface. Total length excluding membrane 5.1–7.7 mm.

Head declivent, broadly rounded apically, jugal margins distinctly sinuate, subparallel for middle third of distance from eyes to apex (see Rolston, 1972, fig. 37); juga equalling or usually slightly surpassing tylus. Length of head from apex to posterior margin of ocellus 1.1–1.5 mm, width across eyes 1.6–2.0 mm. Distance from ocellus to nearest eye equal to or usually greater than twice the diameter of ocellus, distance 0.18–0.22 mm, ocellar diameter 0.07–0.11 mm. Antennal segment 3 much shorter than segments 2, 4, or 5, length of segments 1–5 about 0.2–0.3, 0.5–0.8, 0.4–0.5, 0.5–0.6, 0.7–0.8 mm.

Pronotum 3.6–4.8 mm wide at humeri, mesial length 1.2–1.7 mm. Humeral angle rounded, scarcely produced beyond base of corium. Anterolateral margin of pronotum slightly concave, carinate for posterior half only (see Rolston, 1972, fig. 38). No black on cicatrices.

Scutellum usually slightly wider than long, width at base 2.2–2.9 mm, mesial length 2.1–2.9 mm. Scutellar tongue broader than long, width at base 1.0–1.4 mm, mesial length 0.9–1.3 mm, margins nowhere parallel, tapering to an evenly rounded apex. Width across abdomen nearly as wide as width across humeri. Membrane vitreous, usually with flecks of fuscous scattered along veins.

Ostiolar ruga long, distance from mesial margin of ostiole to apex of ruga greater than distance from apex of ruga to lateral margin of supporting sclerite, ruga evanescent apically, canal not widening apically. Rostral segments 2–4 about 0.8–1.0, 0.5–0.6, 0.5–0.6 mm long.

Posterior margin of pygophore concave on each side of middle with a mesial v-shaped emargination; ventral surface of pygophore without carina. Head of paramere bilobed, lateral lobe small, directed laterally and usually bent weakly toward anterior lobe; anterior lobe bent slightly laterally, narrowed apically (see Rolston, 1972, fig. 42). Female genital plates typical for the genus.

Distribution. Western United States and Mexico.

Etymology. This species is named for the late E. P. Van Duzee, whose work has contributed much to the understanding of this genus and to many other hemipteran genera.

Holotype. UNITED STATES: **Texas:** *Cameron Co.,* Anacua Wildlife Area nr. St. Maria, 6–7 Oct. 1984, D. A. Rider, ♂. Deposited in the National Museum of Natural History, Washington, D.C.

Paratypes. 250 specimens. MEXICO: **Colima:** Armeria Bridge, 3 Sept. 1971, W. D. Nunes & T. F. Halstead, swept weeds, CAS (♂). **Guerrero:** Acapulco, Gro., 20 Aug. 1938, L. J. Lipousky, SMEK (♂). **Oaxaca:** Salina Cruz, 15 July 1952, E. E. Gilbert & C. D. MacNeil, UCB (♂). **Vera Cruz:** with orchids, Brownsville, Tex., 2 Sept. 1960, USNM (♂).

UNITED STATES: **Arizona:** *Maricopa Co.,* Phoenix, LSUC (♂), 3 May 1939, E. E. Russell, *Malva parriflora,* ASUT (♀). *Yuma Co.,* Yuma, 3 May 1951, L. A. Carruth, UAT (♀). **California:** *Kern Co.,* Bakersfield, 7 Apr. 1970, CAS (♀). *Kings Co.,* June 1933, CAS (♀). *Los Angeles Co.,* 4 Apr. 1879, INHS (♀). *Merced Co.,* Gustine, 12 Aug. 1966, T. F. Halstead, CAS (♀). **Colorado:** *El Paso Co.,* Rock Ck. Canyon, Colorado Springs, 30 Aug. 1937, H. H. Ruckes, CAS (♂). *Otero Co.,* Rocky Ford, 14 Sept. 1898, E. D. Ball, UAT (♂). **Kansas:** *Finney Co.,* 15 Aug. 1924, Lawson & Beamer, SMEK (♀); Garden City, July 1896, H. W. Menke, LHR (♂), 12 June 1940, R. H. Beamer, SMEK (3♂♂). *Hamilton Co.,* July, S. J. Hunter, SMEK (♂ 3♀♀). *Meade Co.,* Meade, LSUC (♂). *Morton Co.,* 5 Aug. 1911, F. X. Williams, SMEK (2♀♀); 20 July 1924, C. O. Bare, SMEK (♂); 3 Aug. 1924, SMEK (3♀♀). *Scott Co.,* F. X. Williams, SMEK (♂). *Sherman Co.,* F. N. Williams, SMEK (♂). *Thomas Co.,* Menlo, 23 Aug. 1940, R. H. Beamer, SMEK (♂); F. X. Williams, SMEK (2♂♂ ♀). **Missouri:** *Vernon Co.,* Metz, 21 Apr. 1940, N. L. Wright, UMC (♂). **Nebraska:** *Hayes Co.,* Hayes Ctr., 30 June 1941, on beets, UNL (2♂♂ 4♀♀). *Lancaster Co.,* Lincoln, Mar., UNL (♂). *Scotts Bluff Co.,* Mitchell, 14 July 1915, L. M. Gates, UNL (♀). **Nevada:** *Washoe Co.,* Nixon, 30 June 1927, E. P. Van Duzee, CAS (♀). **New Mexico:** 25 Aug., L. J. Munchmore, LACM (♂). *Sandoval Co.,* Bernalillo, 24 June 1938, R. P. Allen, CAS (♀). **Oklahoma:** *Beaver Co.,* 2 Sept. 1932, W. Davis, LSUC (♂). **South Dakota:** *Brule Co.,* Chamberlain, 24 July 1940, H. C. Severin, under lights, ISU (♂), LHR (♂ ♀). **Texas:** *Bell Co.,* Temple, 22 Aug. 1941, H. S. Dybas, at light, FMNH (♀). *Brazos Co.,* 25 Apr. 1927, R. K. Fletcher, TAMU (♀); College Station, 10 Nov. 1928, S. E. Jones, trap light, TAMU (♂). *Brewster Co.,* Alpine, Sept. 1939, S. E. Jones, ISU (3♂♂

5♀♀), LSUC (♂ ♀); Chisos Mts. Pk., Sept. 1939, S. E. Jones, ISU (♂); Babcock Ranch, 22 mi S Alpine, 26 Aug. 1969, V. V. Board & J. E. Hafernik, LHR (♀), TAMU (2♂♂ ♀). *Brooks Co.,* 25 July 1928, R. H. Beamer, SMEK (3♂♂ ♀); Falfurrias, 21 Aug. 1959, R. B. Selander & J. C. Shaffner, at light, TAMU (♀). *Cameron Co.,* Brownsville, 23 Nov. 1910, INHS (♂ ♀), 17 Dec. 1910, INHS (♂), 9 Oct. 1958, H. V. Weems, Jr., at light, ARH (4♂♂ 4♀♀), 5 Aug. 1973, J. E. Gillaspy, at light, LHR (♀); 6 mi E Brownsville, 14 June 1969, V. V. Board & J. E. Hafernik, TAMU (♀); Palmito Hill, 9 June 1970, V. V. Board, TAMU (♂); Anacua Wildlife Area nr. St. Maria, 6–7 Oct. 1984, E. G. Riley, LHR (16♂♂ 27♀♀), D. A. Rider, AMNH (5♂♂ 5♀♀), DAR (10♂♂ 20♀♀), LSUC (5♂♂ 5♀♀), USNM (5♂♂ 5♀♀). *Comanche Co.,* 15 Apr. 1925, R. H. Beamer, SMEK (♂). *Crockett Co.,* Hwy 349 at Pecos R., 31 May 1973, Gaumer & Clark, TAMU (♀); 24 mi E Iraan, 29 May 1979, Burke, Schaffner, and Friedlander, TAMU (2♂♂ 3♀♀). *Dimmit Co.,* 1 Apr. 1936, S. E. Jones, LSUC (♀); 13 Mar. 1933, S. E. Jones, LHR (♂). *Eastland Co.,* Grace Olive Wiley, 10 Aug. 1920, SMEK (♂). *Hemphill Co.,* Canadian, 10 July 1905, W. M. Mann, FMNH (♂). *Hildago Co.,* 28 July 1928, R. H. Beamer, SMEK (♂ ♀). *Jeff Davis Co.,* 10 mi NW Ft. Davis, 20 July 1968, J. E. Hafernik, TAMU (♂); 25 mi NW Ft. Davis, 20 July 1968, J. E. Hafernik, LHR (♂); 8 mi NE Ft. Davis, 11 Aug. 1968, J. E. Hafernik, TAMU (♀), 10 Aug. 1969, V. V. Board & J. E. Hafernik, TAMU (♂ ♀); 1.5 mi SW Hwy 118 on Hwy 166, 2 June 1983, D. A. Rider, DAR (♀). *Kleberg Co.,* Kingsville, 27 Sept. 1959, SIUC (♂), 13 Sept. 1973, J. E. Gillaspy, LHR (♂). *Motley Co.,* Matador, 15 June 1933, H. G. Johnston, TAMU (3♂♂ 3♀♀). *Pecos Co.,* Ft. Stockton, 23 Oct. 1938, S. E. Jones, LSUC (♀). *Potter Co.,* Amarillo, 5 Sept. 1928, R. H. Fletcher, TAMU (♂). *Presidio Co.,* Plata, 8 June 1968, J. E. Hafernik, TAMU (♂); 3 mi SE Presidio, 20 June 1968, J. E. Hafernik, LHR (♀); 7 mi N Shafter, 22 June 1968, J. E. Hafernik, UCB (♂); Estrada Ck., 8 mi SE Presidio, 9 July 1968, J. E. Hafernik, UCB (♀). *Reeves Co.,* 10 mi SE Pecos, 11 July 1936, R. H. Beamer, SMEK (♀). *Scurry Co.,* Snyder, 22 Aug. 1959, S. Jacobs, UMC (♂ ♀). *Starr Co.,* Falcon Hts., 22 Aug. 1981, R. Turnbow, at light, UGA (♂). *Terrell Co.,* Sanderson, 22 Oct. 1938, S. E. Jones, LSUC (2♀♀). *Val Verde Co.,* Del Rio, 21 Oct. 1938, S. E. Jones, ISU (6♂♂), LHR (♀), LSUC (4♂♂ 3♀♀); Langtry, 21 Oct. 1938, S. E. Jones, ISU (♀), LHR (♂), LSUC (♂ 3♀♀).

Remarks. All the species included in *Tepa* appear quite similar superficially. *Tepa vanduzeei* can be separated from *T. brevis, T. rugulosa,* and *T. yerma* by the longer ostiolar ruga. In *T. jugosa* the ostiolar canal widens apically. *Tepa vanduzeei* is most closely related to *T. panda* from which it can be separated reliably only by the male genitalia. The anterior lobe of the paramere is narrowed apically in *T. vanduzeei*; it is evenly rounded in *T. panda.*

Tepa vanduzeei is the species that most previous workers have called *T. punctiventris.* Most specimens in museums labeled as *T. punctiventris* will probably be this new species.

ACKNOWLEDGMENTS

I would like to thank P. H. Arnaud, Jr., Calif. Acad. Sci., San Francisco for the loan of the type specimens. I would also like to thank the following individuals for the kind loan of specimens (acronyms are those used in the text): R. M. Baranowski, Agr. Res. and Educ. Center, Homestead, Fla. (ARH); R. T. Schuh, Am. Mus. Nat. Hist., New York (AMNH); F. F. Hasbrouck, Ariz. St. Univ., Tempe (ASUT); P. H. Arnaud, Jr., Calif. Acad. Sci., San Francisco

(CAS); G. Mazurek, Field Mus. Nat. Hist., Chicago, Ill. (FMNH); D. J. Voegtlin, Ill. Nat. Hist. Surv., Urbana (INHS); J. Laffoon, Iowa St. Univ., Ames (ISU); C. L. Hogue, Los Angeles Co. Mus. Nat. Hist., Calif. (LACM); J. B. Chapin, La. St. Univ., Baton Rouge (LSUC); L. H. Rolston, La. St. Univ., Baton Rouge (LHR); T. J. Henry, Natl. Mus. Nat. Hist., Washington, D.C. (USNM); P. D. Ashlock, Snow Ent. Mus., Univ. Kans., Lawrence (SMEK); J. E. McPherson, S. Ill. Univ., Carbondale (SIUC); J. C. Schaffner, Texas A&M Univ., College Station (TAMU); F. G. Werner, Univ. Ariz., Tucson (UAT); J. A. Powell, Univ. Calif., Berkeley (UCB); C. L. Smith, Univ. Ga., Athens (UGA); R. L. Blinn, Univ. Missouri, Columbia (UMC); B. C. Ratcliffe, Univ. Nebr., Lincoln (UNL).

I would like to express special thanks to J. B. Chapin and L. H. Rolston for their helpful advice during this study.

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Received August 6, 1985; accepted November 15, 1985.

J. New York Entomol. Soc. 94(4):559–561, 1986

A NEW *PANJANGE* FROM NORTHERN BORNEO (ARANEAE, PHOLCIDAE)

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Abstract.—A new spider, *Panjange sedgwicki,* remarkable for its prolonged eye stalks, is described from Sarawak.

The genus *Panjange* was established by Deeleman-Reinhold and Deeleman (1983) for four new pholcid species discovered by the first author in the foliage of humid forests and on overhanging rocks in Sulawesi, the Philippines, and eastern Borneo. A fifth species was found in the Cape York Peninsula of Queensland, Australia (Deeleman-Reinhold, in press), and recently a close relative of that species was collected in West Irian. Another undescribed species from central Sarawak is described here.

We are indebted to Walter C. Sedgwick for donating this fascinating specimen and to Mohammad U. Shadab for providing the illustrations. All measurements are in millimeters.

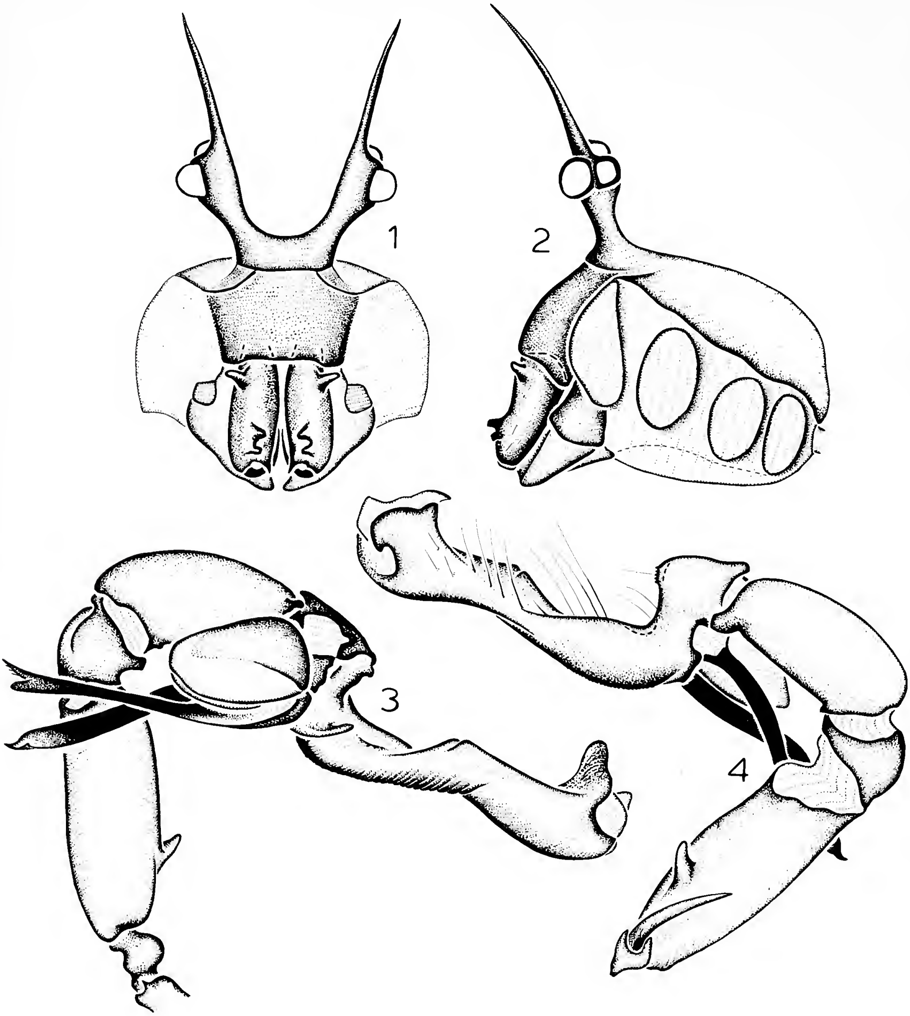
Panjange sedgwicki, new species
Figs. 1–4

Type. Male holotype taken in a forest bordering the Baleh River, 40 miles above Kapit, central Sarawak, Borneo (June 25, 1976; W. C. Sedgwick), deposited in the American Museum of Natural History.

Etymology. The specific name is a patronym in honor of the collector of the holotype.

Diagnosis. This species seems closest to *P. nigrifrons* Deeleman-Reinhold and Deeleman from eastern Kalimantan, but can be distinguished by the presence of long spikes extending dorsally past the eyes (Figs. 1, 2) and numerous parallel chitinous ridges on the ventral surface of the paracymbium (Fig. 3). It differs from all other described males in the shape of the subdistal cheliceral teeth and palpal paracymbium, embolus, and conductor.

Male. Carapace 1.15 long, 1.05 wide; cephalothorax pale yellow except head, clypeus, chelicerae, eye stalks, and palpi pale chestnut brown; eye triads on stalks, white spikes extend above eye stalks for distance equal to 1.3 times stalk height (Figs. 1, 2). Chelicerae each with laterally pointing basal spur, mesoanterior subdistal tooth with two rounded tips, of which most proximal is larger, and medial distal tooth (Fig. 1). Abdomen 4.00 long, white with paired dark spot at half length of dorsum and dark reverse y-shaped mark posteriorly. Legs pale yellow with patellae, tips of femora and tibiae, and base of metatarsi pale chestnut brown.



Figs. 1–4. *Panjange sedgwicki,* new species, male. 1. Frontal view. 2. Cephalothorax, lateral view. 3. Left palp, prolateral view. 4. Left palp, retrolateral view.

	I	II	III	IV	Palp
Femur	11.38	—	5.35	7.68	0.96
Patella	0.58	—	0.48	0.50	0.36
Tibia	11.15	—	4.32	6.50	1.00
Metatarsus	11.56	—	7.10	10.90	—
Tarsus	1.20	—	0.91	1.34	1.88
Total	35.96	—	18.16	26.92	4.20

Palp (Figs. 3, 4) with cymbium 0.34 long, paracymbium 1.54 long, proximal half of ventral surface with row of 20–25 closely spaced parallel chitinous ridges, tip subapically flared; embolus 1.30 long, conductor 1.20 long, both simple, rod-shaped.

Female. Unknown.

Material examined. Only the holotype.

Relationships. Panjange sedgwicki shares with *P. nigrifrons* (plus three other species from western Sarawak to be described elsewhere) the presence of a mesoanterior subdistal tooth on the male chelicerae, an apophysis on the male palpal femur, and a short male palpal cymbium. All these Bornean taxa thus constitute the *nigrifrons* species group. A peculiar, spoonshaped, membranous distal prolongation of the cymbium, reaching almost to the tip of the embolus, is a synapomorphy of the *cavicola* and *lanthana* groups. The *cavicola* group includes both Sulawesi species, *P. cavicola* Deeleman-Reinhold and Deeleman and *P. alba* Deeleman-Reinhold and Deeleman, as well as the Queensland and New Guinea species, which share a curved ocular horn in males and the absence of a subdistal tooth on the male chelicerae. The *lanthana* group includes at present only the type species, *P. lanthana* Deeleman-Reinhold and Deeleman from Luzon, which is set apart by the singular conformation of the male palp, in which the embolus and conductor form a transverse bar attached by its middle to the tip of the bulb.

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Received September 19, 1985; accepted November 27, 1985.

1986

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Journal of the New York Entomological Society

VOLUME 94 OCTOBER 1986 NO. 4

CONTENTS

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