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# IDENTIFICATION OF NEW WORLD AGONUM, REVIEW OF THE MEXICAN FAUNA, AND DESCRIPTION OF INCAGONUM, NEW GENUS, FROM SOUTH AMERICA (COLEOPTERA: CARABIDAE: PLATYNINI) 

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#### Abstract

A key for the identification of the 74 species of Agonum Bonelli in the New World is presented along with taxonomic treatments of the 15 species occurring in Mexico. Neotypes are designated for Agonum orbicollis Say ( $=$ A. punctiforme Say) and Agonum suturale Say. Diagnosis of Agonum based on external characters, and characters of the male and female genitalia and reproductive tract, necessitates removal of South American species previously considered congeneric to a new genus, Incagonum (type species Anchomenus discoculcatus Dejean). Synapomorphies establishing monophyly of Incagonum include reduced subapical elytral sinuation, and female spermatheca with digitate basal lobe. The absence of subapical setae on metatarsomere 4 , and presence of a short but distinct spermathecal duct support the monophyly of Incagonum plus other taxa in the previously proposed Rhadine-Tanystoma lineage. Removal of Incagonum species from Agonum results in restriction of Agonum to lands previously comprising Laurasia, or to regions broadly accreted to its southern margin. Cladistic biogeographic analysis of the Mexican Agonum fauna and other carabid taxa exhibiting Halfter's Nearctic pattern do not contradict a primary division of the Mexican biota into a northern portion, including the Sierra Madre Occidental and Oriental and associated lowland regions, and a southern portion including the Transvolcanic Sierra and Sierra Madre del Sur. The analysis recognizes an area of endemism comprising the southern Sierra Madre Occidental. This area exhibits ambiguous area relationships with areas to the north and south. The included Nearctic pattern taxa also provide only ambiguous information concerning the area relationships for areas north of the Isthmus of Tehuantepec versus the Chiapan highlands.


The carabid genus Agonum is well represented in North America, with 73 species occurring from the Canadian and Alaskan arctic to the montane forests of Chiapas and Nicaragua. Lindroth $(1966,1969)$ provided an excellent treatment of the Canadian fauna, which also serves well for identification of many species found in the United States. Over the recent past (Liebherr, 1984, 1986, 1991a), I have investigated taxonomic relationships within this genus for the New World fauna, as well as relationships of New World taxa to those in the Palaearctic and African regions (unpubl. data). Below, I present a key for identification of Agonum from the New World, and I review those species found within Mexico and Central America. This treatment is intended to complement Lindroth's $(1966,1969)$ faunal work, and will allow accurate identification of Agonum species from throughout their range in the New World.

A number of South American species have been described and placed in the genus

Agonum. Examining 20 of these species for a cladistic analysis of Agonum of the world (unpubl. data) indicated that their similarity to Agonum is based on symplesiomorphy. Because they present numerous synapomorphies absent from the rest of Agonum and present in several other genera of Platynini, and lack derived character state combinations characterizing the various species groups of Agonum, I describe the new genus Incagonum to accommodate the named South American taxa, and remove to this genus those species for which I have examined type specimens.

The realignment of South American "Agonum" in Incagonum results in the zoogeographic provenance of Agonum being restricted to lands that constituted Laurasia, or montane regions in areas such as India, southern China, and southeast Asia that have been accreted to its southern edge. The major possible exception to this generalization involves African species, such as Agonum rufoaeneum Reiche and Agonum (Agonidium) kenyense Alluaud, found in montane areas of eastern Africa. These species form a basal clade within the genus, and based on as yet unstudied relationships to taxa closely related to Agonum, may or may not be best classified as members of the genus (unpubl. data). Association of east African montane regions with an otherwise Holarctic taxon is also observed in the genus Calathus (Casale, 1988).

## DIAGNOSIS OF $A G O N U M$

Lindroth (1966) used a very broad definition of Agonum, which included taxa now placed in other genera such as Platynus (Whitehead, 1973; Liebherr, 1989a), Anchomenus (Liebherr, 1991b), Sericoda (Liebherr, 1986, 1991b), and Oxypselaphus (=Anchus) (Liebherr, 1986). Specimens to be identified with this work can be distinguished by the diagnosis provided below, and names of genera included by Lindroth (1966) under Agonum, but currently excluded, may be determined by consulting Liebherr (1986:177). This diagnosis and others make use of a cladistic analysis (unpubl. data) to determine whether certain traits are primitive or derived.

Diagnosis. Head capsule not strongly constricted dorsally behind eyes, dorsal transverse impression not visible in lateral view. This trait will serve to distinguish Agonum from most Platynus species. Pronotal basal seta present (absent in A. kenyense Alluaud of Africa, A. reluscens Andrewes of India, and A. galvestonicum Casey and A. quadrimaculatum Horn from North America); pronotal lateral seta present. Pronotum with convex or sinuate basolateral margins, the hind angles obtuse-angulate to totally rounded and obsolete; if basolateral margins are sinuate and hind angles well developed, then lateral margins are narrow and non-explanate in apical half of pronotum. Pronotal disc with transversely stretched isodiametric mesh to more transverse mesh microsculpture (except extensicolle group with isodiametric mesh microsculpture; A. cyanope Bates, A. extimum Liebherr, A. parextimum Liebherr, $A$. texanum LeConte, A. extensicolle Say, A. decorum Say, and A. elongatulum Dejean from North America). Third elytral interval with 3-16 setae in or adjacent to it. Elytral apex not denticulate, rounded at suture and at subapical sinuation. Metafemora with from one to many setae on anteroapical surface (absent in punctiforme group; A. crenistriatum LeConte, A. pallipes F ., A. punctiforme Say , A. rigidulum Casey, and A. rufipes Dejean from North America; and $A$. reluscens). Penultimate metatarsomere with outer subapical seta present or absent; inner seta present (absent only in $A$. reluscens, A. semicupreum from China, some individuals of the Palaearctic $A$. gracilipes Duftschmid, and A. quadrimaculatum, which also lack outer seta). Apical


Figs. 1-3. Scanning electron micrographs of Incagonum discosulcatum. 1. Left third to fifth metatarsomeres, dorsal view, $79 \times$. 2. Left gonocoxa, ventral view, showing apical fringe of basal gonocoxite and apical gonocoxite, $348 \times$. 3 . Apical depression of apical gonocoxite, bearing two long nematiform setae and two short, bluntly-rounded furrow pegs, $3075 \times$.
tarsomere with from four to eight setae in two ventral rows (setae small but still visible in $A$. excavatum Dejean, A. crenulatum LeConte and A. striatopunctatum Dejean, setae absent in A. errans Say, A. ferreum Haldeman and A. sulcipenne Horn, all from North America). Male aedeagal internal sac with fields of darker microspicules or with only pale microtrichia, lacking well-developed spicules or spines. Female gonocoxae with apical fringe of six or more setae on penultimate segment; two to four lateral ensiform setae on apical gonocoxite.

## MONOPHYLY AND RELATIONSHIPS OF AGONUM

Monophyly of Agonum is based on pronotal shape, with cladistically basal taxa in the genus exhibiting straight to convex basolateral margins. The sinuate basolateral margins, as observed in A. extensicolle (Fig. 17), are secondary reversals to the primitive state of this character. The genus is also characterized by the derived medial absence of a basal pronotal marginal bead. This character is also reversed within the genus, with a median basal bead present in species such as $A$. anthracinum (Fig. 10) and $A$. pacificum (Fig. 35). Derived absence of the outer subapical seta on the fourth metatarsomere also supports monophyly, although as in the other characters, this setal loss is reversed in a number of members of the genus. Monophyly is also supported by characters of the female spermatheca. The spermatheca of Agonum is primitively comprised of a narrow basal duct and apical spermathecal reservoir. The spermathecal duct is primitively only one to two times as long as the apical reservoir, but may be up to $10 \times$ as long in its most derived condition (Liebherr, 1986: fig. 4).


Figs. 4-6. Male aedeagal median lobe with internal sac distended, ventral view. Horizontal scale $\mathrm{bar}=0.50 \mathrm{~mm}$. 4. Incagonum discosulcatum. 5. I. brasiliense. 6. Female reproductive tract of I. discosulcatum, ventral view. Vertical scale bar $=0.50 \mathrm{~mm} . \mathrm{bc}=$ bursa copulatrix; $\mathrm{bdp}=$ basal digitate process of spermatheca; $\mathrm{gc}=$ gonocoxa (incompletely drawn); $\mathrm{sg}=$ spermathecal gland; $\mathrm{sp}=$ spermatheca .

These derivations from the primitive condition of nondifferentiated cylindrical spermatheca, as seen in the sister subtribe Sphodri (Liebherr, 1986: figs. 2b, c; Casale, 1988: figs. 91, 94-97), are shared with the genus Platynus. This derived similarity in spermathecal configuration supports sister group status for Agonum and Platynus,
both of which are placed in the subtribe Platyni. To differentially diagnose these genera, Agonum exhibits a derived condition of more or less orbicular pronotal shape, and Platynus possesses the derivation of constricted neck lacking in Agonum.

## Incagonum, new genus

Type species: Anchomenus discosulcatus Dejean, 1828.
I will revise this genus in a subsequent publication, and therefore restrict this presentation to a differential diagnosis permitting recognition of member taxa, followed by a discussion of the synapomorphies supporting monophyly, and likely most closely related taxa.

Diagnosis. Head capsule elongate; neck constricted laterally behind eyes, not constricted dorsally and so transverse dorsal impression not visible from lateral view. Basal pronotal marginal bead absent medially; pronotal basolateral margins sinuate, to straight, to convex before well-indicated hind angles; pronotal laterobasal depressions smooth, not rugose or punctate, without raised tubercles. Elytra with basal groove rounded at humerus; subapical sinuation nearly obsolete, the lateral margin evenly convex from median length to rounded apex at suture; sixth and seventh striae reduced, fifth stria also reduced in I. discosulcatum (except in I. fuscoaeneum Gemminger and Harold and I. quadricolle Dejean, with all striae equally developed). Body surface brunneous to piceous, shiny or matte, but not metallic; pronotal disc with transverse mesh microsculpture, elytra with transverse microsculpture, surface iridescent in some taxa (except I. fuscoaeneum and I. quadricolle with isodiametric elytral microsculpture). Fourth metatarsomere lacking both inner and outer subapical setae (Fig. 1).

Male genitalia. Parameres subequal, dorsal or left paramere broadly rounded apically, ventral or right paramere narrower, but still rounded apically. Aedeagal median lobe smooth medially, without wrinkles (Fig. 4); median lobe evenly curved to straight medially, but never recurved; lobe apex acuminate to narrowly rounded, evenly curved (Fig. 4) to more abruptly downcurved (Fig. 5). Aedeagal internal sac with evident spicules (Figs. 4, 5) (spicules very small in I. pedestre Putzeys).

Female reproductive tract. Spermathecal duct short, spermatheca with apical reservoir and a shorter basal digitate process (Fig. 6). Basal gonocoxite with apical fringe of setae (Fig. 2); apical gonocoxite with two to three lateral and one dorsal ensiform setae, apical depression bearing two nematiform setae and two furrow pegs (Fig. 3).

## MONOPHYLY AND AFFINITIES OF INCAGONUM

Monophyly of Incagonum is supported by two synapomorphies. The two genericlevel synapomorphies include reduced subapical sinuation of the elytra; a character otherwise uncommonly observed in the Platynini, and a basal digitate process of the female spermathecal reservoir; uniquely derived in Platynini. Other platynine taxa exhibit a bipartite spermathecal reservoir; e.g., some species in the genus Glyptolenus (Liebherr, 1988: fig. 4d). But, the relative sizes of the spermathecal components differ greatly between these taxa, and at present the basal digitate process of Incagonum and the larger apical spermathecal bulb of Glyptolenus are not considered homologous.

Several other derived character states are also present in Incagonum species so far examined. The presence of a short spermathecal duct is a derived state that Incagonum species share with species of Rhadine and Tanystoma, distinguishing them from those taxa that possess the primitive configuration of cylindrical ductless spermatheca; i.e., many taxa of the subtribe Sphodri, as well as genera of the subtribe Platyni such as Atranus (Liebherr, 1986: fig. 2g) and Paranchodemus (Liebherr, 1989b). Agonum and Platynus species generally exhibit longer spermathecal ducts than Incagonum, Rhadine, and Taynstoma, suggesting that Agonum and Platynus form a separate clade. Both the inner and outer subapical setae are absent from the fourth metatarsomere of Incagonum species, a condition also observed in species of Rhadine and Tanystoma (Liebherr, 1989b). Absence of subapical setae is also observed in several species of Agonum; however, based on the sum of information from all characters, those species are nested well inside the cladistic limits of that genus. Finally, Incagonum discosulcatum females possess two furrow pegs in the apical depression of the apical gonocoxite (Fig. 3), a configuration shared with species of Rhadine, but not Tanystoma or Paranchodemus (Liebherr, 1989b, c), which exhibit six to nine furrow pegs. Agonum placidum Say has four furrow pegs in the apical depression, and Platynus decentis Say possesses six setae (unpubl. data). Whether the state of two furrow pegs observed in Rhadine and Incagonum is symplesiomorphous or synapomorphous remains to be determined.

Based on the absence of both inner and outer subapical tarsal setae and a female spermatheca with a short duct, Incagonum is provisionally considered a member of the Rhadine-Tanystoma lineage, sensu Liebherr (1986). These last two genera are of Nearctic distribution, but this lineage would appear to have a much broader geographic distribution. Other generic-level taxa that are characterized by absence of subapical setae and a short-ducted spermatheca include Ctenognathus from New Zealand, Cardiomera from around the Mediterranean, Disenochus from the Hawaiian Islands, and an unnamed genus from Fiji (B. P. Moore, pers. comm.). Therefore, at present I could not exclude any area of the world as potentially housing the sister group to Incagonum.

## CHECKLIST OF INCAGONUM

I have examined the types of the following taxa, thereby permitting me to place them in the genus Incagonum. All species possess the diagnostic synapomorphies listed above.

Incagonum, new genus
aeneum Reiche, 1843 [NEW COMBINATION].
quitense Bates, 1891; synonymy (Moret, 1988).
ambiguum Solier, 1849 [NEW COMBINATION]. andicola Bates, 1891 [NEW COMBINATION]. angulatum Chaudoir, 1854 [NEW COMBINATION]. bonariense Gemminger and Harold, 1868 [NEW COMBINATION].
angustatum Dejean, 1831 (not Dejean, 1828).
brasiliense Dejean, 1828 [NEW COMBINATION]. chilense Dejean, 1831 [NEW COMBINATION].


Figs. 7-12. Pronota. 7. Agonum punctiforme. 8. A. patinale. 9. A. cyclifer. 10. A. anthracinum. 11. A. scutifer. 12. A. suturale.
distinctum Solier, 1849 [NEW SYNONYMY]. circumdatum Erichson, 1834 [NEW COMBINATION]. coquimbanum Gemminger and Harold, 1868 [NEW COMBINATION]. chilense Solier, 1849 (not Dejean).
cordicolle Solier, 1849 [NEW COMBINATION]. dejeani Solier, 1849 [NEW COMBINATION]. discosulcatum Dejean, 1828 [NEW COMBINATION]. fuscoaeneum Gemminger and Harold, 1868 [NEW COMBINATION].
fuliginosum Dejean, 1831 (not Panzer).
gayi Solier, 1849 [NEW COMBINATION]. lineatopunctatum Dejean, 1831 [NEW COMBINATION].
melas Solier, 1849 [NEW COMBINATION]. pedestre Putzeys, 1878 [NEW COMBINATION]. quadricolle Dejean, 1828 [NEW COMBINATION]. semistriatum Fairmaire, 1883 [NEW COMBINATION].

Csiki (1931:846-847) lists five other species from South America in combination with Agonum: geniculatum Motschulsky, 1864; haemorrhoum Perty, 1830; inaequale Putzeys, 1875; luczoti Laporte, 1834; and quadripustulatum Dejean, 1831. I have not examined types of these taxa, but restriction of reliably recognized Agonum to areas north of and including Nicaragua casts doubt on these combinations, and I suggest that these species, once examined carefully, will be found members of Incagonum or some other clade of South American Platynini. I have examined the type of the only other species from South America listed by Csiki (1931:847)Anchomenus triseriatus Chaudoir, 1854-and it is hereby removed to Platynus [NEW COMBINATION].

## KEY TO NEW WORLD SPECIES OF AGONUM

This key is drawn from that of Lindroth (1966), and includes additional Agonum species in the United States and Mexican faunas recognized since his ground-breaking work. I exclude species in taxa subsequently distinguished from Agonum, but which Lindroth included in his broad concept of the genus. Such excluded genera are Platynus (Whitehead, 1973; Liebherr, 1989a); Anchomenus, Sericoda, and Tetraleucus (Liebherr, 1991b); Tanystoma (Liebherr, 1985); and Rhadine, Paranchus, and Oxypselaphus (=Anchus) (Liebherr, 1986). In this key, species names followed by an asterisk occur in Mexico, with species treatments included in this work. Species names preceded by a number, or followed by a page number only, are treated in Lindroth (1966, 1969). For species described in yet other sources, the appropriate citation follows the species name. Figures noted in lower case (i.e., "fig.") are those found in Lindroth (1966), whereas figures designated with a capitalized legend are found in this work. This key is best used with Lindroth's work as a companion.

1. Third antennal segment at least in apical half with short pubescence in addition to apical ring of longer setae (fig. 290b) ..... 2$1^{\prime}$. Third antennal segment only with occasional setae in addition to apical ring oflonger setae (fig. 290a)22
2(1). All, or the alternate, elytral intervals with seta-bearing punctures (setae sometimes short but clearly visible in lateral view) ..... 3


Figs. 13-18. Pronota. 13. Agonum cyanope. 14. A. extimum. 15. A. parextimum. 16. A. texanum. 17. A. extensicolle. 18. A. decorum.

2'. Elytra only with the ordinary seta-bearing dorsal punctures on third interval
3(2). Only alternate elytral intervals with seta-bearing, very coarse punctures. Head and prothorax glabrous. Antennae and legs black
29. A. belleri

3'. All elytral intervals with small seta-bearing punctures. Also head and prothorax $\pm$ pubescent. Legs and at least base of antennae pale
4(3). Ventral body surface with pelage of fine setae. Eight to 16 erect dorsal macrosetae in or adjacent to third elytral interval A. extimum*
$4^{\prime}$. Ventral body surface with only a few fine setae in addition to macrosetae. Eightor fewer dorsal elytral setae in or adjacent to third elytral interval
A. decorum* (red-hirsute and green-hirsute morphs)
5(2). Elytra bicolored, black with base and a large post-median spot bright red. Posterior lateral seta-bearing puncture of prothorax lacking 61. A. quadrimaculatum
5'. Elytra without pronounced color pattern. Prothorax with two lateral pore-punc- tures ..... 6
6(5). Head capsule and pronotal disc vividly metallic blue or green. Pronotal margins concolorous or paler ..... 7
6'. Head capsule and pronotum piceous to brunneous, not strongly metallic ..... 9
7(6). Pronotum metallic green on disc, testaceous along lateral margins and in baso- lateral depressions, microsculpture of transverse meshes. $6.0-7.2 \mathrm{~mm}$
23. A. anchomenoides
7'. Pronotum uniformly metallic blue or green, microsculpture of granulate isodia- metric meshes. $7.1-10.1 \mathrm{~mm}$ ..... 8
8(7). Upper body surface metallic blue to purple; legs piceous. Pronotal lateral margins straight to slightly sinuate before hind angles (Fig. 13) A. cyanope*
$8^{\prime}$. Upper body surface metallic green; legs testaceous. Pronotal lateral margins clearly sinuate before hind angles (Fig. 15) A. parextimum*
9(6). Elytra iridescent from fine, parallel micro-lines, not confluent into meshes. Eighth stria deeply impressed along its whole length 16. A. darlingtoni
$9^{\prime}$. Elytra not iridescent, microsculpture consisting of isodiametric or slightly trans- verse meshes. Eighth stria shallower, at least at middle ..... 10
10(9). Meta-tarsi (besides one or two lateral grooves, as usual) with median furrow (figs. 295a, b) ..... 11
10'. Meta-tarsi smooth or rough medially, but without median furrow ..... 12
11(10). Segments 2-4 of antennae darker than fifth and following segments. Microsculp- ture meshes of elytra somewhat irregular 11. A. gratiosum
11'. Antennae without conspicuous color contrasts. Microsculpture of elytra isodia-metric13. A. thoreyi
12(10). Basal pore-puncture of prothorax lacking. Head (fig. 296c) with small but very convex eyes and very long temples. ..... 17. A. galvestonicum
$12^{\prime}$. Prothorax with two lateral setigerous punctures, as usual. Eyes larger and less convex, temples shorter (figs. 296a, b) ..... 13
13(12). Upper surface (including elytral epipleura) black, usually with metallic luster. Antennae and legs black (exceptionally first antennal segment and tibiae dark piceous) ..... 14
13'. Elytral epipleura pale (testaceous to piceous), at least in apical part. Legs (in superioris sometimes only basal $2 / 3$ of tibiae) and usually antennae $\pm$ pale ..... 16
14(13). Prothorax (fig. 291a) without trace of hind angles. Microsculpture of elytra iso- diametric without tendency of transverse arrangement ..... 5. A. simile
14'. Prothorax with obtuse but at least suggested hind angles. Microsculpture meshes of elytra more irregular, at least in part $\pm$ transverse, with tendency of forming transverse rows ..... 15
15(14). Prothorax (fig. 291c) with distinct hind angles, sides straight or slightly sinuate in basal half. Outer antennal segments very short ..... 7. A. exaratum
15'. Prothorax (fig. 291b) only with suggested hind angles, sides never sinuate
6. A. consimile
16(13). Prothorax pale as the elytra, contrasting against the black head. Femora and tibiaetestaceous
14. A. lutulentum
16'. At least the disc of prothorax as dark as the head. Legs often darker ..... 17
17(16). Basal setigerous puncture of prothorax removed from lateral margin. Third basalantennal segments (except in a rare aberration) pale. Wings often reduced
10. A. retractum
17'. Basal setigerous puncture of prothorax touching lateral margin. Antennae darker (at least base of third segment darker than second). Wings full ..... 18
18(17). Eyes very convex. Prothorax (fig. 294a) with very obtuse but evident hind angles. Dorsal punctures larger 8. A. picicornoides
18'. Eyes flatter. Hind angles of prothorax disappeared, not evident. Dorsal punctures very small ..... 19
19(18). Prothorax (fig. 294d) large with broad, oblique depression inside hind angles, greatest width about middle. Upper surface of body unicolorous, dark12. A. superioris
19'. Prothorax (figs. 296a, b) smaller, more constricted at base, laterobasal depression narrower, greatest width before middle. Forebody usually darker than elytra ..... 20
20(19). Eyes convex (fig. 296a). Prothorax quadrate 9. A. sordens
20'. Eyes small and flat (fig. 296b) to moderately convex. Prothorax more elongate ..... 21
21(20). Elytral microsculpture isodiametric. Basal two antennal segments pale, third seg- ment darker 15a. A. canadense (p. 1119)
21'. Elytral microsculpture strongly transverse. Basal three antennal segments usually pale 15b. A. palustre (p. 1119)
22(1). The four outermost antennal segments abruptly pale, yellow to white 46. A. albicrus
22'. Antennae without such color contrast ..... 23
23(22). Last (claw-bearing) tarsal segment glabrous underneath (or with up to four in- conspicuous setae near apex, notably in errans) ..... 24
23'. Last tarsal segment with two parallel rows of long setae underneath ..... 29
24(23). Prothorax (fig. 320b) strongly cordate with protruding, somewhat acute hind an- gles. Black, legs pale with dark knees. $7-8 \mathrm{~mm}$ long (S. Appalachians to northern Florida) A. sulcipenne Horn
24'. Prothorax broader, less constricted at base, hind angles obtuse or rounded ..... 25
25(24). The three dorsal punctures of elytra strongly foveate ..... 55. A. excavatum
25'. Dorsal punctures small, non-foveate ..... 26
26(25). Prothorax (fig. 31la) very broad, lateral depression evident to front angle
47. A. errans
26'. Prothorax narrow (figs. 312, 315b), convexity of disc almost reaching side-margin in frontal half ..... 27
27(26). Hind angles of prothorax not evident (fig. 312c). Elytral straie finely punctate A. crenulatum (p. 619)
27'. Hind angles very obtuse (figs. 312b, 315b) but still evident. Elytral striae strongly punctate ..... 28
28(27). Elytra uneven, transversely impressed at about middle, and longitudinally im- pressed at tip of fifth stria. Legs entirely pale 50. A. striatopunctatum
28'. Elytra not impressed. Femora almost black 56. A. ferreum
29(23). Elytra yellow, darker along the suture, often broadly so (up to five or six intervals). No metallic reflection ..... 30
29'. Elytra unicolorous, black to brown (or in variolatum, with foveate dorsal punc- tures, pale with infuscated disc) ..... 31
30(29). Body size 4.9-6.3 mm. Very narrow. Prothorax with suggested hind angles, hardly wider than head (fig. 298) 18. A. nigriceps
30'. Body size $>7.5 \mathrm{~mm}$. Prothorax with disappeared hind angles, almost circular, much wider than head A. pallipes (p. 620)
31(29). Elytra with three (exceptionally, unilaterally or at least irregularly placed, with four) rather small, never foveate dorsal punctures ${ }^{1}$ ..... 32
31'. Elytra with at least four dorsal punctures (if, exceptionally, only three, usually on one side only, then clearly foveate) ${ }^{1}$ ..... 63
32(31). Prothorax (fig. 314) with very small, deep, punctiform laterobasal depressions (almost circular in form, hind angles not evident) ..... 33
$32^{\prime}$. Prothorax with broader, less defined laterobasal depressions, often with a $\pm$ linear impression internally. ..... 37
33(32). Elytra with shallow impression at middle (on the level of second dorsal puncture). Prothorax only little wider than head. Upper surface with metallic hue
54. A. aeruginosum
33'. Elytra without median impression. Prothorax much wider than head. Unmetallic upper body surface ..... 34
34(33). Elytral striae coarsely punctate, punctures visible to apex (notably in outer striae). Elytra and sternites without microsculpture 51. A. crenistriatum
34'. Elytral striae with fine punctures, disappearing well before apex. Elytra usually, sternites always bearing microsculpture ..... 35
35(34). Prothorax with pronounced convexity outside laterobasal depression (Fig. 7, fig. 314a). Microsculpture of $q$ evident on entire forebody, on the elytra of the $\delta$ consisting of transverse lines fusing into $\pm$ transverse meshes. Femora often in- fuscated 53. A. punctiforme*
35'. Prothorax $\pm$ depressed outside laterobasal depression. Microsculpture of forebody $\pm$ obsolete medially, on the elytra isodiametric or entirely lacking. Legs entirely pale ..... 36
36(35). Microsculpture of elytra in both sexes irregularly isodiametric, with meshes tend- ing to form transverse rows. Elytra short with rounded sides . . A. rigidulum (p. 621)
36'. Microsculpture of elytra lacking in the $\delta$, in the $\%$ regularly isodiametric withouttendency of transverse arrangement. Elytra more elongate and parallel-sided
52. A. rufipes
37(32). Legs entirely pale testaceous ..... 38
37'. Legs darker (at least piceous or black) ..... 40
38(37). Hind angles of prothorax completely disappeared (fig. 312d). Entire upper body surface metallic blue or green. ..... A. basale (p. 620)
38'. Hind angles evident though very obtuse (figs. $299 \mathrm{~b}, \mathrm{c}$ ). At most forebody $\pm$ metallic39
39(38). Basal metatarsomere with evident internal furrow. Prothorax (fig. 299b) broad, widening anteriorly with pronounced depression along sides in basal half
39'. Basal metatarsomere not (or extremely faintly) furrowed internally. Prothorax (fig. 299c) very narrow with almost no depression along side margin
21. A. ferruginosum
40(37). Prothorax (fig. 299c) narrow, only slightly wider than head. Subapical sinuationof elytral margin very weak (fig. 300c). Not metallic. $5.5-7.0 \mathrm{~mm}$ (W half of NAmerica)21. A. ferruginosum
40'. Prothorax much wider than head. Subapical sinuation of elytra evident. Most specimens larger ..... 41
41(40). Base of prothorax margined laterally, the elevated bead clearly delimited (either immediately inside posterior lateral seta or closer to median line) ..... 42

[^1]41'. Base of prothorax without well-defined bead, though often indistinctly raised laterally ..... 49
42(41). 6.5-8.2 mm. Prothorax with evident hind angles (fig. 306m). Elytra with $\pm$ piceous ground color at least apically, quite unmetallic although slightly iridescent due to microsculpture ..... 43
42'. Usually larger. Hind angles of prothorax almost lacking. Elytra black, almost constantly with metallic (often brilliant) luster ..... 44
43(42). Elytral striae coarsely punctate in basal half, smooth apically. Elytral intervals convex, microsculpture of transverse meshes to rows of transverse lines
A. imitans Notman (see Liebherr, 1991a)
43'. Elytral striae with only traces of fine punctulae. Elytral intervals nearly flat, mi- crosculpture of slightly transversely stretched isodiametric meshes
43. A. propinquum*
44(42). Raised basal bead of prothorax directly connected in the region of posterior pore- puncture with the equally well-defined lateral bead ..... 45
44'. Basal head of prothorax well defined only inside basal foveae, lateral bead ob- scurely defined, or lacking ..... 48
45(44). Meshes of elytral microsculpture joined into transverse rows. Upper surface at most with faint metallic hue ..... 36. A. affine
45'. Microsculpture of elytra consisting of isodiametric or very slightly stretched mesh- es, without transverse arrangement. Upper surface (with extremely rare individual exceptions) metallic ..... 46
46(45). Pronotal basolateral margin convexly expanded posteriorly, median pronotal basal margin inflexed (Fig. 10). Pronotum blue to purple, with granulate isodiametric microsculpture A. anthracinum*
46'. Pronotal basolateral margin not strongly expanded posteriorly, basal margin straight medially, evenly curved to hind angles. Pronotum shiny metallic aeneous to green, transverse microsculpture not granulate ..... 47
47(46). First antennal segment, tibiae, and elytral epipleura $\pm$ pale. Metallic luster of elytra uniform. Microsculpture meshes of elytra in part slightly transversely stretched
47'. Appendages and elytral epipleura black (or almost so). Elytra usually with metallic color different on center and laterally. Microsculpture meshes of elytra quite iso- diametric 25. A. suturale* (considered $A$. subsericeum by Lindroth)
48(44). Elytra clearly metallic, usually with strong color contrast between disc and sides.Shoulders angulate, prominent24. A. cupripenne
48'. Upper surface black (elytra sometimes with violaceous hue). Shoulders broadly rounded, not prominent ..... A. cyclifer*
49(41). Upper surface with vivid, usually contrasting metallic luster, greener on forebody, brassy on elytra; or entire body green. Tibiae yellow (except at apex), femora almost black in apical half 26. A. muelleri
49'. Upper surface pure black or elytra (rarely prothorax) with faint metallic hue. Less (or no) color contrast between femora and tibiae ..... 50
50(49). Elytra with $\pm$ pronounced depression along apical part of fifth stria ..... 51
$50^{\prime}$. Elytra without (or with faintest suggestion of) such depression ..... 56
51(50). First antennal segment bright rufous (at least underneath). Prothorax with sides and base diaphanously piceous. Entire elytral epipleura pale ..... 52
51'. First antennal segment black or piceous. Prothorax at most with sides very nar- rowly piceous. Epipleura rarely entirely pale ..... 53
52(51). Prothorax (fig. 306k) with sides reflexed but without defined lateral bead (at leastin basal half). Elytral intervals absolutely flat41. A. moerens
52'. Prothorax (fig. 3061) with thin, clearly defined lateral bead, reaching basal seta (or almost so). Elytral intervals usually $\pm$ convex
42. A. deceptivum

## 53(51). Prothorax (fig. 306c) without any trace of hind angles; margin rather broadly

 elevated around posterior setigerous puncture. Upper surface shiny black35. A. corvus
53'. Prothorax (figs. $306 \mathrm{~g}-\mathrm{i}$ ) with suggested though very obtuse hind angles; margin
there less elevated. At least elytra constantly with metallic hue ............... 54
54(53). First antennal segment (at least underneath) and elytral epipleura $\pm$ pale (less so in British Columbia). Basal pore puncture causing a small jag at the margin of prothorax, whereby the hind angle protrudes as a small, blunt denticle (sometimes almost imperceptible)
36. A. harrisi
54'. Antennae entirely black. Hind angle of prothorax without evident denticle. Elytral apex more pointed, subapical sinuation more evident
55(54). Lateral depression of prothorax $\pm$ interrupted by a prolonged convexity of the disc, forming anterior limit of basal fovea. (Pacific coast)
37. A. brevicolle
55'. Lateral depression of prothorax not interrupted (Transamerican) 37. A. metallescens
56(50). Elytral epipleura and tibiae (at least in more than basal half, sometimes entire legs), often also pronotal epipleura rufous or piceous
56'. Elytral epipleura and tibiae black (or the latter piceous at base), pronotal epipleura black, to faintly piceous at notopleural suture ..... 60
57(56). Hind angles of prothorax evidently denticulate (fig. 306a), basal foveae rather strongly punctate 31. A. melanarium
57'. Hind angles of prothorax virtually disappeared, basal foveae impunctate (or almost so) ..... 58
58(57). Pronotal and elytral microsculpture granulate (sculpticells raised), of slightly trans- versely stretched isodiametric meshes. Dorsal body surface appearing dull
A. patinale*
58'. Pronotal and elytral microsculpture of transverse meshes, not granulate. Dorsal body surface shiny ..... 59
59(58). Body size $8.0-9.5 \mathrm{~mm}$. Elytral striae with rudiments of punctulae ..... 40. A. tenue
$59^{\prime}$. Body size $7.2-8.7 \mathrm{~mm}$. Elytral striae strongly punctate A. collare (p. 612)
60(56). Upper surface almost constantly with metallic hue; elytra not iridescent, theirmicrosculpture consisting of short, in part almost isodiametric meshes. (Pacificcoastland)38. A. brevicolle
$60^{\prime}$. Upper surface pure black; elytra slightly iridescent, their microsculpture consisting of transverse lines, joining into $\pm$ transverse meshes ..... 61
61(60). Sides of prothorax broadly explanate (fig. 306b). Shoulders angulate and produced
38. A. trigeminum
61'. Sides of prothorax less explanate. Shoulders rounded, little produced ..... 62
62(61). Prothorax with a minute jag at hind angle. Outer segments of antennae more than twice as long as wide. Tibiae usually piceous at base 34. A. fidele
62'. Prothorax without jag at hind angle. Outer antennal segments less than twice as long as wide. Legs entirely black 33. A. mutatum
63(31). Dorsal punctures of elytra clearly foveate, each surrounded by a depression with a diameter at least nearly equal to the width of third interval ..... 64
63'. Dorsal punctures not (or very much less) foveate ..... 66
64(63). Elytra pale, brown, yellowish along sides (but without strong contrasts). Forebody dark with faint metallic hue. (Western) 22. A. variolatum
64'. Entire upper body surface dark, usually vividly metallic ..... 65
65(64). Antennae and legs black. Prothorax without lateral bead. Upper surface very shiny, elytra without sharp color contrasts. (Northern) 28. A. quinquepunctatum
65'. Antennal base and legs rufous. Prothorax with thin but clearly defined lateral bead. Upper surface dull, inner elytral intervals aeneous, the outer bright green. (Eastern) 27. A. octopunctatum
66(63). Hind angles of prothorax $\pm$ obtuse but not entirely rounded (least evident in fossigerum, fig. 301d), sides just in front of them straight or sinuate ..... 67
66'. Hind angles of prothorax entirely rounded, virtually disappeared (least so in tex- anum, fig. 317d), sides in front of them rounded ..... 80
67(66). Body non-metallic. Elytra with almost no sinuation of side-margin before apex (fig. 300c) 21. A. ferruginosum
67'. At least part of upper surface with $\pm$ pronounced metallic luster. Elytra with evident subapical sinuation ..... 68
68(67). Prothorax bright red, strongly contrasting against the dark, greenish head
A. decorum* (red-glabrous morph)
68'. Prothorax darker, not contrasting ..... 69
69(68). Legs and more than first antennal segment pale (testaceous to rufous) ..... 70
69'. At least tarsi darker, at most first antennal segment quite pale ..... 72
70(69). Prothorax (Fig. 17, figs. 317a, b) very narrow; front angles protruding. Entire upper surface metallic blue to green70'. Prothorax (figs. 299a, b) more widened before middle; front angles rounded. Atmost forebody clearly metallic.71
$71(70) .3$ to 5 , usually 4 , small dorsal elytral punctures. Elytral subapical sinuation shallow (fig. 300b). Second antennal segment hardly darker than third ...... 20. A. piceolum
71'. 5 to 6 , sometimes 7, slightly foveate dorsal elytral punctures. Subapical sinuation of elytra well developed (fig. 300a). Second antennal segment piceous at tip, darker than third 19. A. bicolor
72(69). Elytra very flat, uneven in apical third, with shallow depression both near the suture and along apical part of fifth stria. Disc of elytra aeneous, shiny; lateral margins with more granulate microsculpture, green A. fallianum (p. 598)
72'. Elytra more convex, without depression on disc although apex of fifth stria maybe depressed. Disc of elytra with same microsculpture and color as lateral areas73
73(72). Hind angles of pronotum rounded (fig. 301d). Basal pronotal marginal bead lacking medially, hind margin of pronotum thick. Head and pronotum black, with only a trace of aeneous metallic sheen A. fossigerum (p. 596)
73'. Hind angles of pronotum evident. Basal margin of pronotum thin, not elevated above level of scutellum. Head and pronotum metallic green, or with aeneous, cupreous or violaceous metallic sheen ..... 74
74(73). Apex of second antennal segment with ring of 6-8 setae. Lateral margin of pro- notum sinuate before hind angles (fig. 317c) ..... 75
74'. Apex of second antennal segment with single seta on outer surface (one to two small setae may accompany large outer seta). Lateral margin of pronotum straight before hind angles ..... 78
75(74). Males, with expanded protarsomeres 1 to 3 bearing spatulate adhesive setae ven- trally. Abdomen with four apical setae ..... 76
75'. Females, with protarsomeres 1 to 3 bearing only two parallel rows of spinose setae ventrally. Abdomen with two apical setae ..... 7776(75). Discriminant function score, measurements in $\mathrm{mm}(-10.8-[12.9 \times$ prothoraciclength $]-[4.1 \times$ maximum elytral width $]+[7.3 \times$ elytral length $])<0.213$.Prothorax with lateral margins sinuate before hind angles (Fig. 18). Body size 6.9-8.0 mmA. decorum* green-glabrous morph
76'. Discriminant function score $>0.213$. Prothorax with lateral margins convex to
sinuate before hind angles. Body size 7.1-8.8 mm
A. elongatulum (see Liebherr, 1986:137)
$77(75)$. Discriminant function score, measurements in $\mathrm{mm}(-11.6-[10.7 \times$ prothoraciclength $]+[1.7 \times$ maximum elytral width $]+[4.9 \times$ elytral length $])<0.199$.Prothorax with lateral margins sinuate before hind angles (Fig. 18). Body size 6.9-9.2 mmA. decorum* green-glabrous morph
77'. Discriminant function score $>0.199$. Prothorax with lateral margins convex to sinuate before hind angles. 8.7-9.2 mm . . . A. elongatulum (see Liebherr, 1986:137)
78(74). Basal margin of pronotum indistinctly raised near hind pronotal seta and behindbasolateral depressions. $7.5-9.0 \mathrm{~mm}$A. muiri (see Liebherr, 1984)
78'. Basal margin of pronotum clearly defined in vicinity of hind pronotal seta and behind basolateral depressions (it may be broad in suturale). $8.2-11.0 \mathrm{~mm}$ ..... 79
79(78). Elytra with four setae in or adjacent to third interval. Striae with evident punctulae25. A. suturale* (considered A. subsericeum by Lindroth)
79'. Elytra with five to eight setae in or adjacent to third interval. Striae smooth, punctulae not well developed A. pacificum*
80(66). Antennae and legs black. Elytral epipleura and ventral body surface metallic, aeneous 30. A. cupreum
80'. At least basal antennal segment underneath and tibiae $\pm$ pale. Elytral epipleura rufous to piceous at least apically, paler than ventral body surface ..... 81
81(80). Sides of prothorax evidently and rather widely reflexed (inside the raised bead), also before middle. Entire upper surface with faint blue or green luster (often more evident on prothorax but not different in color) ..... 82
81'. Sides of prothorax not (or extremely narrowly) reflexed in anterior half. Forebody with aeneous or green, elytra with bronzy or brassy luster ..... 85
82(81). Pronotal basolateral margins strongly expanded posteriorly (Figs. 10, 11) ..... 83
82'. Pronotal basolateral margins not or only weakly expanded posteriorly (Figs. 9, 16) ..... 84
83(82). Pronotum (Fig. 11) broadly convex to lateral margins even in apical half, robust. Humeri sharply angulate ..... A. scutifer*
83'. Pronotum (Fig. 10) depressed inside lateral marginal bead in apical half, less robust. Humeri tightly rounded to slightly angulate A. anthracinum*
84(82). Pronotum (fig. 310a) small with moderately rounded sides. Humeri angulate,produced; elytral intervals flat (or almost so)44. A. placidum*
84'. Pronotum (Fig. 9, fig. 310b) much broader with more rounded sides. Humeri broadly rounded, striae stronger, intervals clearly convex ..... A. cyclifer*
85(81). Pronotum (fig. 312a) very narrow with slightly rounded sides and obsolete hindangles. Elytral intervals flat49. A. nutans85'. Pronotum (Fig. 16, fig. 317d) much broader with more rounded sides and suggestedhind angles. Intervals somewhat convexA. texanum*

## REVIEW OF THE MEXICAN FAUNA OF $A G O N U M$

For each species occurring in Mexico, I have listed the original combinations of all synonyms, and type localities, designations, and depositories. For brevity's sake, I have not provided complete synonymies; I provide them for the extensicolle group (Liebherr, 1986). Consultation of references listed in the "types" sections will provide information on recent taxonomic actions dating from 1955. The expanded specieslevel diagnostic combinations include salient external characters, and features of the male genitalia and female genitalia and reproductive tract. For those species restricted to Mexico and neighboring portions of the United States or Central America, I have
listed all material examined, whereas for species with broader ranges, Mexican material is listed, and extralimital records summarized. A section on flight wing configuration is included for those species exhibiting wing polymorphism.

The species are listed under species groups defined by a cladistic analysis based on 119 characters for 128 taxa of Agonum from throughout the Holarctic range of the genus (unpubl. data). These groups differ somewhat from Liebherr (1986:177), and the classification makes use of the nomenclatural decisions on species groups and associated types species of associated subgeneric names summarized in Lindroth (1966). The full results of the cladistic analysis will be published elsewhere. For present purposes, diagnoses of groups containing Mexican species are presented. These diagnoses are lists of synapomorphies and shared-derived character states for all but one of the species groups. Both permit definition of species-group membership, with the synapomorphies substantiating monophyly of the species groups. The melanarium species group is a paraphyletic assemblage of taxa, and its diagnosis is a combination of shared-derived characters-synapomorphies at higher taxonomic rank-and symplesiomorphies. For the diagnoses, synapomorphies at the species group taxonomic rank are indicated by an asterisk ( ${ }^{*}$ ), synapomorphic reversals to the primitive state at the species group rank are indicated by a reverse arrow ( $\leftarrow$ ), shared-derived character states serving as synapomorphies at taxonomic ranks more inclusive than the species group are indicated by a caret ( ${ }^{\wedge}$ ), and symplesiomorphies are indicated by a dagger ( $\dagger$ ).

## punctiforme species group <br> (subgenus Circinalia Casey, 1920; type punctiforme Say)

Species group diagnosis. Neck shortened, not constricted or elongate ( ${ }^{\wedge}$ ); pronotum orbicular (Fig. 7), sides convex ( ${ }^{\wedge}$ ); pronotal basal angles rounded ( $\wedge$ ); pronotal lateral margins narrow (*); pronotal laterobasal depressions pitlike, surrounded by raised area $\left(^{*}\right)$; elytral striae weakly punctate $\left(^{*}\right) ; 8$ th elytral stria impressed entire length $(\leftarrow)$; metafemora apex anteriorly glabrous $(\leftarrow)$.

## Agonum punctiforme Say

## Feronia punctiformis Say, 1823:58.

[Agonum saltuum Sturm, 1826:89. Invalid name listed only in catalog without indication.]
Agonum orbicollis Say, 1830:[3] (see Bousquet, 1993).
Agonum foveicolle Chaudoir, 1843:764.
[Agonum rotundicolle Sturm, 1843:23. Invalid name listed only in catalog without indication.]
Olisares picipes Motschulsky, 1864:326.
Circinalia ludovicianum Casey, 1920:76.
Types. Of punctiforme, neotype ồ (Lindroth and Freitag, 1969), Philadelphia Neck, PA (MCZ); of orbicollis, original type series destroyed, neotype $q$, "Mexico-Hidalgo, 35 km NE Zimapán, 1 June 1948, 7,200', pine oak scrub/collected by: F. G. Werner, W. L. Nutting" (MCZ), hereby designated; of foveicolle, lectotype $\%$ (Lindroth, 1966), New Orleans, LA (MNHP); of picipes, lectotype ô (Liebherr, 1991a), Caracas, Ven-


Figs. 19-25. Aedeagal median lobe with internal sac distended, ventral view. All to same scale. 19. Agonum punctiforme. 20. A. patinale. 21. A. cyclifer. 22. A. anthracinum. 23. A. scutifer. 24. A. placidum. 25. A. suturale.


Fig. 26. Mexican distributional records for Agonum punctiforme.
ezuela (MSUM); of ludovicianum, lectotype ô (Lindroth, 1975), Alexandria, LA (NMNH).

Diagnosis. Pronotal hind angles rounded, with slight widening of marginal bead at basal setae (Fig. 7); laterobasal depressions bounded laterally by convex portion of disc. Elytra with well-developed transversely stretched isodiametric microsculpture; well-developed isodiametric microsculpture on abdominal sternites and metepisternum. Legs rufobrunneous, tibiae rufotestaceous, slightly paler than sternites and concolorous with pale elytral epipleura. Body length $7.5-8.9 \mathrm{~mm}$.

Male aedeagus with very faint wrinkles on euventral surface of median lobe (Fig. 19); median lobe evenly curved with acuminate apex; parameres and median lobe near parameral articulation piceous, apex paler.

Female reproductive tract with spermathecal duct $2 \times$ as long as apical reservoir, duct tightly looped just below insertion of spermathecal gland duct at base of reservoir (see Liebherr, 1986: fig. 4e). Basal gonocoxite with apical fringe of about eight setae; apical gonocoxite with two lateral and one dorsal ensiform setae.
Distribution. Found throughout the eastern United States and southern Ontario and Quebec, Canada (Lindroth, 1966). It is present on the island of Bermuda (AMNH, MCZ ), probably as an adventive introduction. I have seen specimens from California localities including: San Mateo Co., Mt. San Bruno (RENC); La Grange, Stanislaus

Co. (CDFA); Sacramento, Sacramento Co. (CDFA); Pomona, Los Angeles Co. (UCRC); Riverside, San Jacinto, and near Thermal, Riverside Co. (LACM, UCRC); Escondido, San Diego Co. (UCRC); and Calexico, Imperial Co. (UCRC). Mexican localities include several in Sonora state, and one in Chihuahua (Fig. 26), as well as localities in the eastern and central states from Nuevo Leon to México and eastern Jalisco. The Chiapan populations appear isolated from populations over the rest of the range, as also observed in Agonum texanum (Fig. 45).

Mexican and middle American material. GUATEMALA. - intercepted ex orchid, Guatemala on Pan-Am (NMNH, 1). MÉXICO.-Chiapas: Amatenango del Valle, pasture-lake (UASM, 24); El Rosario, NW of Comitán (UVMC, 2); Laguna Chamula microondas S Rte. 190, 2,340 m, oak-pine for., meadows (UASM, 1); Rancho Nuevo, 6 mi SE San Cristobal de las Casas, pine woods (UVMC, 26), 8.6 mi E San Cristobal de las Casas, 7,900 ft (UASM, 1), 79-9,200 ft (UASM, 3); San Cristobal de las Casas (CNC, 1; UVMC, 1), 69-7,100 ft (UASM, 21), 7,000 ft (UASM, 17), 7, 200 ft (CNC, 1), Rte. 190, 7,900 ft (UASM, 4), 1 mi , trail to ruins (UVMC, 1), 7 mi E, berlese (CNC, 7; UVMC, 1), 8 mi SE, Rte. 190 (UVMC, 8), 8.6 mi E, Rte. 190, 7,900 ft (UASM, 14), $10 \mathrm{mi} E, 8,300 \mathrm{ft}$, in bromeliads (UASM, 1), 3 mi W, $7,300 \mathrm{ft}$ (UASM, 1), 3.4 mi W, Rte. 190 (UASM, 3), 4.4 mi W, Rte. 190 (UMMZ, 1), 9 km W , Rte. 190, 2,390 m, oak-pine for., Alnus litter (UASM, 2); San Juan de Chamula (UVMC, 9); Tenejapa, 8 mi NE San Cristobal de las Casas (CNC, 1). Chihuahua: Santa Clara (BMNH, 1). Guanajuato: Guanajuato (BMNH, 1). Hidalgo: Zimapán, 35 km NE, $7,200 \mathrm{ft}$, pine-oak scrub (MCZ, 8). México: Toluca, 34 km W , Rte. 15, 8,500 ft, creek margin (UASM, 3). Michoacán: Morelia, 1,886 m (UMMZ, 6); Pátzcuaro (NMNH, 1). Nuevo Leon: Montemorelos, 11.7 mi W, Rte. 85, 1,550 ft (UASM, 4); Monterrey, Chipinque Mesa, 4,000 ft (UASM, 5). San Luis Potosí: Alvarez Mtns. [=Alvarez, 35 km SE San Luis Potosí] (BMNH, 1); Santa Catarina, 15 mi W, Rte. 86, 6,200 ft (UASM, 1). Sonora: Ciudad Obregón (CNC, 7); Imuris, 19.3 km N , 1,040 m (UASM, 19); Navojoa (CISC, 1). Tamaulipas: La Pesca, 9.9 mi W, UV light (UASM, 2).

Ecology. The broad geographic range is paralleled by broad ecological tolerance in this species. Specimens have been taken along creek margins, in Alnus litter in pine-oak forests, in pine-oak scrub, in bromeliads, and along a pasture lake. Specimens have also been collected at black light.

## cyclifer species group

Species group diagnosis. Neck shortened, not constricted or elongate (^); pronotum wide ( $\wedge$ ); pronotal margins convex, hind angles rounded ( $)$; pronotal basal margin expanded posteriorly behind laterobasal depressions (*); elytral microsculpture isodiametric and granulate $\left(^{*}\right)$; male aedeagus with median lobe straight in apical half ${ }^{*}$ ).

## Agonum patinale Bates

Anchomenus patinalis Bates, 1882:95.
Type. Lectotype \&, "Cuernavaca/Mexico, Sallé Coll./B.C.A. Col. I. I., Anchomenus


Fig. 27. Distributional records for Agonum patinale ( $\star=$ district record only).
patinalis, Bates/Lectotype (purple circle)/Lectotype Agonum patinale (Bates), J. K. Liebherr 1984." (BMNH), hereby designated.

Diagnosis. Distinguished from other members of the species group by the small body size-length $6.9-9.2 \mathrm{~mm}$-and granulate isodiametric microsculpture across upper body surface. Pronotum with broad, slightly wrinkled laterobasal depressions, evenly elevated to meet lateral margin, marginal bead therefore lacking at rounded basal angles (Fig. 8). Elytra with two to three (in one example unilaterally four) setae in third interval; intervals moderately convex. Head and pronotum piceous; elytra dark brunneous, elytral epipleura rufobrunneous, paler than piceous sternites; femora piceous at middle, tibiae and tarsi slightly paler.

Male aedeagal median lobe with wrinkled euventral surface (Fig. 20); lobe straight in apical half, apex bluntly rounded.

Female reproductive tract with very elongate spermathecal duct, about $6 \times$ as long as apical reservoir; apical reservoir with about 10 weak beadlike constrictions. Basal gonocoxite with apical fringe of six to seven setae; apical gonocoxite with two lateral and one dorsal ensiform setae.

Distribution. A. patinale is the only Agonum to be found in Central America, and in Mexico is found in Chiapas, in higher elevations of Guerrero to Nayarit, and in the Transvolcanic Sierra (Fig. 27).

Material examined. EL SALVADOR.-Ahuachapán: Bosque, El Imposible, 745 m (CAS, 1). San Salvador: Los Planes, Puerto del Diablo, 1,000 m (CAS, 1). MÉX-

ICO.-Chiapas: Frontera Comalapa, 7.7 mi N, $2,600 \mathrm{ft}$ (UASM, 1). Distrito Federal: Mexico City (AMNH, 1). Guerrero: Chilpancingo, 8.4 mi W, $4,900 \mathrm{ft}$ (UASM, 2). Jalisco: Nevado de Colima, SE slope (CAS, 1). México: Temascaltepec, Real de Arriba (MCZ, 3). Morelos: Cuautla, 11.5 mi W, Rte. $115 \mathrm{D}, 4,500 \mathrm{ft}$ (UASM, 1); Cuernavaca, 9 mi N, 8,500 ft (CUIC, 1). Nayarit: Bella Vista (UASM, 1). NICARAGUA. - Chontales (BMNH, 1).

Ecology. This species is uncommonly collected, and little is known of its ecological preference. Collection localities, for which the elevations are known, range from 7452,600 m.

## Agonum cyclifer Bates

Anchomenus cyclifer Bates, 1884:281.
Platynus arizonensis Horn, 1892:42.
Types. Of cyclifer, holotype $\ddagger$, Mexico City (MNHP); of arizonensis, lectotype $\widehat{\delta}$ (Liebherr, 1991a), Camp Grant, AZ (MCZ).

Diagnosis. Pronotum with lateral margins evident at basal setae, as in the following two species, but with basal marginal bead weak to absent medially (Fig. 9); basal margin moderately posteriorly expanded behind laterobasal depressions. Humeri narrowly rounded, elytra with convex lateral margins; four setae in third interval. Flight wings constantly macropterous. Upper body surface piceous; elytral epipleura concolorous with rufopiceous sternites, legs concolorous to slightly darker. Body length $9.0-10.8 \mathrm{~mm}$.

Male aedeagus smooth on euventral surface (Fig. 21); median lobe straight in apical half, apex narrowly acuminate.

Female reproductive tract with spermathecal duct about $2 \times$ length of apical reservoir; apical reservoir fusiform, without beadlike constrictions. Basal gonocoxite with apical fringe of 11-12 setae; apical gonocoxite with one or two lateral and one dorsal ensiform setae.

Distribution. This species is broadly restricted to the Rio Grande Valley, neighboring bolsons and river valleys in northern Mexico, and the lowlands of southeastern Arizona (Fig. 28).

Material examined. MÉXICO.—Durango: Villa Lerdo (BMNH, 8; MCZ, 4; NMNH, 1). Nuevo Leon: San Roberto, 52.5 mi S, Rte. 57, $5,400 \mathrm{ft}(\mathrm{UASM}, 1), 9.9 \mathrm{mi}$ N, Rte. 57, 1,600 m (UASM, 1). San Luis Potosí: Ciudad del Maiz, 7.5 mi NW (CAS, 4). U.S.A.-Arizona: Santa Rita (CAS, 1). Cochise Co.: Chiricahua Mtns., (UAZC, 1), Portal, 5 mi W, SW Res. Sta., $5,400 \mathrm{ft}$ (AMNH, 2); Dragoon (CAS, 1); Huachuca Mtns., Carr Cyn. 15 mi S Sierra Vista, 5,600-6,000 ft (CNC, 1), Parker Cyn. Lk., $5,500 \mathrm{ft}$ (UAZC, 3), Ramsey Cyn. (UAZC, 1); Sulphur Springs Vy. (CAS, 1; NMNH, 18). Pima Co.: Arivaca, Arivaca Ck. (CAS, 1); Tucson, 26.5 mi W, Rte. 86, 3,400 ft (CUIC, 14). Santa Cruz Co.: Nogales, 10 mi E (AMNH, 1); Patagonia (NMNH, 2). New Mexico: San Juan Co.: Chaco Cyn. Nat. Mon., 6,200 ft, desert shrub (CNC, 1). Texas: Jeff Davis Co.: Davis Mtns. (CAS, 2), Davis Mtns. St. Pk., 5,200 ft (CUIC, 7). Presidio Co.: Marfa, 11 mi W (CISC, 1). Terrell Co.: Dryden (AMNH, 6).

Ecology. Found around water sources at elevations of $1,000-1,600 \mathrm{~m}$. West of Tucson in August (CUIC), I found it on the muddy clay banks of a flooded creekbank, with other carabids of the genera Calosoma, Megacephala, Bembidion, Pterostichus,


Fig. 28. Distributional records for Agonum cyclifer.

Polpochila, Selenophorus, and Stenolophus. In April (CUIC), beetles were found overwintering along Limpia Creek in the Jeff Davis Mountains under downed logs away from the creek edge, and in loose soil with roots and a few rocks along an arroyo bank.

Agonum anthracinum Dejean, 1831:739.
Type. Lectotype, đ九, " ${ }^{\prime}$ " (green sex label)/anthracinum m in Mexica/Höpfner/LECTOTYPE, Agonum anthracinum Dej., det. George E. Ball 1972" (MNHP), hereby designated.

Diagnosis. Pronotum with basolateral margin evident at basal seta, basal margin broadly posteriorly expanded behind laterobasal depressions (Fig. 10); basal marginal bead evident medially. Humeri angulate; elytra domelike, depressed at sides and apex; elytral intervals moderately convex; three to five setae in third interval. Flight


Fig. 29. Distributional records for Agonum anthracinum.
wings dimorphic, macropterous or vestigial (see below). Upper body surface coal black, often with blue or purple metallic sheen, especially on elytra; elytral epipleura dark basally, paler apically; femora piceous, concolorous with sternites; trochanters, tibiae, and tarsi paler, rufopiceous. Body length $8.4-12.9 \mathrm{~mm}$.

Male aedeagal median lobe strongly wrinkled (Fig. 22); lobe straight in apical half, apex acuminate; parameres piceous, median lobe piceous near parameral articulation, paler near apex.
Female reproductive tract with elongate spermathecal duct, about 3-4× as long as apical reservoir, duct tightly coiled near base of reservoir; reservoir moniliform, with 9-11 beadlike constrictions. Basal gonocoxite with apical fringe of 10 thick setae set close together; apical gonocoxite with two to three lateral and one dorsal ensiform setae.

Distribution. Found in Transvolcanic Sierran and montane western Mexico north of the Isthmus of Tehuantepec, north to the lowlands of the Cochise filter/barrier of southeastern Arizona (Fig. 29).
Material examined. MÉXICO.-Chihuahua: La Polvosa, 6,400 ft (AMNH, 1); Madera, 13 mi SE, Rte. 16, 2,100 m (UASM, 1); Yecora, 9.6 km S (Son.), 1,750 m (UASM, 1). Colima: Colima, 16.5 mi E, Rte. $110,1,900 \mathrm{ft}$ (UASM, 1), 8 mi SW , impoundment (UASM, 1). Distrito Federal: Mexico City (BMNH, 1; MCZ, 1). Durango: Durango (MCZ, 1). Guanajuato: Guanajuato (BMNH, 1); Leon, 6.3 mi NW,

Rte. 45, 6,700 ft (UASM, 1). Guerrero: Amula, 6,000 ft (BMNH, 1); Chilapa (CNC, 1); Chilpancingo, 59 km N, Filo de Caballo Rd., $1,890 \mathrm{~m}$, oak for. litter (UASM, 2), $8.4 \mathrm{mi} \mathrm{W}, 4,900 \mathrm{ft}$ (UASM, 5); Ixtapán de la Sal, 27 km SE, 1,463 m (UASM, 1); Rte. 134, 78.5 km N jct. Rte. 200, 1,770 m, ridge top, pine-oak (UASM, 1); Xochipala, 15 km SW, $1,800 \mathrm{~m}$, green grassy ridgetop (CMNH, 1). Hidalgo: Guadelupe (MCZ, 5). Jalisco: Ajijic, mtns. and cn. N, 5,400 ft, scrub forest (UASM, 1); Cuautla, 5.5 mi NW, 6,600 ft (UASM, 1); El Rincon, 30.5 mi NW Los Volcanes, 5,400 ft (UASM, 2); Guadalajara (CMNH, 2), 8 mi NW (UCRC, 4); Jiquilpan (Michoacán), 10 mi W (SW) (CAS, 15); Ocotlán, Lake Chapala (CAS, 1); Talpe de Allende, $6.5 \mathrm{mi} \mathrm{S}, 4,340$ ft (UASM, 4); Tequila, 9.6 km S , microondas rd., $1,970 \mathrm{~m}$, oak-pine litter (UASM, 1). México: Atlacomulco, $5 \mathrm{~km} \mathrm{~N}, 2,650 \mathrm{~m}$ (UASM, 1); Temascaltepec, Real de Arriba (BMNH, 1; MCZ, 1), 6,000-7,000 ft (BMNH, 1), Tejupilco (CAS, 1), 4,000 ft (BMNH, 1). Michoacán: Apatzingán, 7.2 mi S (OHSC, 1); Gabriel Zamora, 2.3 km N, 756 m , trop. decid. for., pasture (UASM, 4); Jiquilpan, 10 mi W (UASM, 3); Morelia, 9.5 mi W, Rte. 15, 6,250 ft, trop. decid. for. (UASM, 1), E, Rte. 15, 7,000 ft , creek \& arid pasture (UASM, 3); Villamar, 8.1 mi E, Rte. $15,5,500 \mathrm{ft}$ (UASM, 9). Morelos: (BMNH, 1; CAS, 1); Cuautla, 11.5 mi W, Rte. $115 \mathrm{D}, 4,500 \mathrm{ft}$ (UASM, 1); Cuernavaca (BMNH, 3; CAS, 4; MCZ, 6), pedregal (UASM, 1), $5,000 \mathrm{ft}$ (NMNH, 1), $5.4 \mathrm{mi} \mathrm{E}, 4,600 \mathrm{ft}$, pedregal (UASM, 3), $9 \mathrm{~km} \mathrm{E}, 5,000 \mathrm{ft}$, (MCZ, 1), 9.1 mi E , $4,300 \mathrm{ft}$ (UASM, 1); Santa Rosa, 3.2 mi N Zacatepec, 3,100 ft (UASM, 1); Xochicalco, 4,000 ft (UASM, 1). Nayarit: Santa Maria del Oro, 3 mi NW (CISC, 1). Oaxaca: Juchatengo, 21.8 mi N, $7,100 \mathrm{ft}$ (UASM, 1); Las Peras [=San Miguel Peras, 24 km SW Oaxaca] (BMNH, 1); Microondas 0.5 km E jct. Rtes. $190 \& 125,2,529 \mathrm{~m}$ (UASM, 1), oak for. (dry) (UASM, 2); Monte Alban (UASM, 1; UVMC, 10); Oaxaca (UVMC, 6), $5,000 \mathrm{ft}$ (CAS, 1); Ojo de Agua road, 15.7 km S Rte. 190, 2,320 m, oak-pine zone, Alnus nr. stream (UASM, 7); Santa Catarina Juquila, 12.8 mi E, pine-oak forest (UASM, 1). Queretaro: Pinal de Amoles, 6.4 mi E, $6,000 \mathrm{ft}$ (UASM, 1). Sinaloa: Concordia, 61.7 km E, Rte. 40, 1,889 m, oak-pine-madrone, pine chips (UASM, 1); El Palmito, 1.5 km W, Rte. 40, 1,920 m, oak-pine-madrone, leaf litter (UASM, 1), $1,970 \mathrm{~m}$ (UASM, 1), $5 \mathrm{mi} \mathrm{W}, 6,100 \mathrm{ft}$ (MSUC, 1); Mazatlán, 113 km E, Rte. 40, $1,980 \mathrm{~m}$, pine-oak litter (UASM, 2), 125.5 km E, Rte. $40,2,000 \mathrm{~m}$, pine-oak litter (UASM, 4). Sonora: Huachinera, $14 \mathrm{~km} \mathrm{~S}, 1,150 \mathrm{~m}$, acacia grassland (UASM, 3); Mesa de Tres Ríos, 2 km N, 1,950 m, oak-pine for. (UASM, 1); San Nicolas, E, rd. to La Angostura, 1,400 m, grassland, oak forest (UASM, 1); Yecora, 7,000 ft (CNC, 1), 6.4 km NE, rd. to Maycoba, $1,548 \mathrm{~m}$ (UASM, 1). Veracruz: Córdoba (BMNH, 1); Las Vigas (BMNH, 1). U.S.A.-Arizona: (NMNH, 1). Cochise Co.: Chiracahua Mtns., Sunny Flat (CNC, 1); Douglas, 8 mi E, Geronimo trail (CNC, 1); Huachuca Mtns., Couper Cyn., SW end, 6,000 ft (UAZC, 2); Garden Cyn. (MCZ, 1; NMNH, 1), Parker Cyn. Lk., $5,500 \mathrm{ft}$ (UAZC, 1); San Pedro R. at Palomenas, $4,500 \mathrm{ft}$ (CNC, 2).

Ecology. This species has been recorded from habitats between 750 and 2,650 m elevation. These include pine-oak or pine-oak-madrone forests, where it has been found in litter. It also occurs in grassland areas bordering forests, along creeks, and in pastures.

Flight-wing condition. The flight wings of this species are dimorphically developed, either fully macropterous, or reduced to a vestigial flap that does not extend beyond the end of the metanotum. Based on the material at hand, the frequency of brachyptery varies across the range, being most commonly observed in regions of the Transvol-


Fig. 30. Percentage of specimens of the wing-dimorphic Agonum anthracinum with fully developed flight wings (number of specimens in each regional sample in parentheses).
canic Sierra (Fig. 30), with the macropterous condition prevailing around the periphery of the range in Veracruz, Oaxaca, Durango and Sinaloa, and Arizona. However, an anomalously high frequency of brachypters in Chihuahua and Sonora disrupts this pattern, and greater numbers of specimens are needed to determine whether flight-wing development in this species is determined by broad-scaled or localized factors.

## Agonum scutifer Bates

Anchomenus scutifer Bates, 1878:594.
Type. Lectotype \&, "Mexico/Anchom. scutifer Bates/Lectotype/Lectotype, Anchomenus scutifer Bates, George E. Ball, 1972," hereby designated.

Diagnosis. Most robust species of the group; pronotum domelike, front angles protruding, lateral margins depressed relative to elevated disc; marginal bead broad


Fig. 31. Distributional records for Agonum scutifer.
and flat at basal setae; basal margin broadly posteriorly expanded behind laterobasal depressions (Fig. 11). Elytra with tightly rounded angulate humeri, basal groove strongly curved inside humeral angles; elytral intervals usually flat; four to six setae in third interval, rarely one to five setae in fifth interval. Flight wings dimorphic, most frequently vestigial, rarely macropterous (see below). Upper body surface with strong, granulate isodiametric microsculpture, coal black with blue to purple metallic sheen on pronotal base and elytra; ventral body surface and legs concolorous, piceous, elytral epipleura only slightly paler towards apex. Body length $8.9-12.6 \mathrm{~mm}$.

Male aedeagal median lobe smooth euventrally, basally curved, straight in apical half before slightly downturned acuminate apex (Fig. 23); parameres and median portion of median lobe only slightly darker than lobe apex.

Female reproductive tract with spermathecal duct less than $2 \times$ length of apical reservoir, duct coiled at base of reservoir; reservoir weakly moniliform, about 10 beadlike constrictions present; basal gonocoxite with apical fringe of seven setae; apical gonocoxite with three lateral and one dorsal ensiform setae.

Distribution. Found throughout the Sierra Madre Occidental and Transvolcanic Sierra (Fig. 31).

Material examined. MÉXICO.-(CAS, 2; MCZ, 3). Chihuahua: Cerro Venado 37 km N Temosachic, 2,161 m (UASM, 8); Colonia Garcia, 2,130 m, meadow \& pineoak for. (UASM, 35), $3 \mathrm{~km} \mathrm{~N}, 2,080 \mathrm{~m}$ (UASM, 2), $13.2 \mathrm{~km} \mathrm{~N}, 1,900 \mathrm{~m}$, meadow


Fig. 32. Percentage of specimens of the wing-dimorphic Agonum scutifer with fully developed flight wings (number of specimens in each regional sample in parentheses).
nr. ck. (UASM, 2); Ejido Zaragoza, $7.4 \mathrm{~km} \mathrm{~N}, 2,110 \mathrm{~m}$ (UASM, 2), 15.2 km N , 2,150 m, meadow (UASM, 6); Madera, 7.6 mi SE, Rte. $16,2,050 \mathrm{~m}$ (UASM, 6); Majalca, 45 mi NW 7,000 ft (CNC, 1); Mesa del Huracán (CNC, 1); Miñaca, 6,400 ft (UASM, 2); Parrita, 27 mi W, Llano de Río Santa Clara (AMNH, 1); San Pablo Balleza, 31 km SE, $2,050 \mathrm{~m}$, grassland, oak-acacia (UASM, 16). Distrito Federal: (NMNH, 1); Cuajimalpa, under stones (NMNH, 3); Mexico City (BMNH, 1). Durango: Coyotes, Durango dist. (AMNH, 1); Durango, 37 mi W, $8,400 \mathrm{ft}(\mathrm{MCZ}, 20)$, 39 mi W, 8,600 ft (UASM, 7), 72 km W, Rte. 40, 2,540 m, oak-pine (UASM, 1); El Salto, Cruz de Piedra, 2,350 m (DmMC, 3), 6 mi NE, 8,500 ft (AMNH, 1), 6.4 km E, 2,800 m (UASM, 1), 23.2 mi E, Rte. 40, 7,500 ft (UASM, 1); Los Puentes, 7,500 ft (AMNH, 1); Refugio (MCZ, 1; NMNH, 1); Reserva de la Biosfera, La Michilia, Trampa Las Casas, 2,500 m, pine-oak forest (UASM, 1), 5 km S Trampa Las Casas, 2,500 m, El Temescal meadow (UASM, 14), Trampa Piedra Herrada, 2,500 m, meadow/oak for., pitfalls (UASM, 1); Rte. $10 \mathrm{~km} \mathrm{90}, \mathrm{2,470} \mathrm{m} ,\mathrm{meadow} \mathrm{nr}. \mathrm{pine-}$ oak for. (UASM, 3). Hidalgo: Tizayuca, 5 mi N (CAS, 3). Jalisco: Jiquilpan (Michoacán), 10 mi W (CAS, 13); Lago de Moreno, 13 mi SE, Rte. 45, 6,450 ft, reservoir
(UASM, 2). México: El Yukón, Rte. 15 W Toluca, $8,800 \mathrm{ft}$ (UASM, 1); Rte. 57, km 127, high desert (CUIC, 3); Toluca (AMNH, 2; BMNH, 2; CAS, 11; MCZ, 18), 34 km W, Rte. $15,8,500 \mathrm{ft}$, creek margin (UASM, 2). Michoacán: Morelia, 9.5 mi W , Rte. 15, 6,250 ft, trop. decid. for. (UASM, 17); Tzintzuntzan vic., 7,000 ft, nr. roadside (UASM, 1). Puebla: Puebla (BMNH, 1); Tlaxco (Tlaxcala), 28 km N, Rte. 119, 2,300 m, wet pasture (UASM, 7). Veracruz: Jalapa (BMNH, 2); Las Vigas (BMNH, 2).

Ecology. Found from 1,900-2,800 m elevation, in pine-oak forest, wet pastures, and meadows.

Flight-wing condition. Most A. scutifer individuals are brachypterous; however, low frequencies of macropterous individuals have been examined from localities in Chihuahua and Jalisco (Fig. 32). Macropterous individuals are not randomly distributed among collected series. Of the 13 specimens from Michoacan, the only 2 macropterous beetles comprised the series from Lago de Moreno. And, of the 4 macropters of the 83 specimens known from Chihuahua, 3 form part of the series of 16 from San Pedro Balleza. This suggests that factors of very limited geographic scope may influence flight-wing configuration in this species.

## melanarium species group <br> (subgenus Melanagonum Casey, 1920; type melanarium Dejean)

Species group diagnosis. Basolateral pronotal margins straight or convex, not sinuate ( ${ }^{\wedge}$ ); basal pronotal margin not expanded posteriorly behind basolateral depressions ( $\dagger$ ); elytral microsculpture isodiametric to transverse, but not granulate (except A. albicrus) ( $\dagger$ ); cuticle non-metallic, piceous, at most with iridescent luster ( $\dagger$ ); profemur with 2 anteroventral setae and 3 posterior setae ( ${ }^{\wedge}$ ); mesofemur with 3-6 anteroventral setae ( ${ }^{\wedge}$ ); metafemur with 3-4 anteroventral setae ( ${ }^{\wedge}$ ).

Agonum propinquum Gemminger and Harold
Agonum piceum LeConte, 1848:226 (not Linné).
Platynus propinquus Gemminger and Harold, 1868:375 (replacement name for piсеит LeConte).
Platynus fraterculus LeConte, 1869:373.
Anchomenus xanthocnemis Bates, 1884:281.
Agonum humile Casey, 1920:117.
Agonum insueta Casey, 1920:118.
Agonum amens Casey, 1924:83.
Types. Of piceum, type locality Massachusetts (MCZ), $\gtrdot$ labelled "type" (MCZ) is from Canada, and therefore not a true type (Lindroth, 1966); of fraterculus, holotye 9, Vancouver Island, BC (MCZ); of xanthocnemis, holotype $\uparrow$ (Liebherr, 1991a), Mexico state, Mexico (BMNH); of humile, lectotype ô (Lindroth, 1975), Kalispell, mt ; of insueta, lectotype $\ddagger$ (Lindroth, 1975), Wilbur, WN; of amens, lectotype ó (Lindroth, 1975), Edmonton, AT.

Diagnosis. In the Mexican fauna, distinguished by the small size, body length 6.58.2 mm , the angulate pronotal hind angles with a minute jag (Lindroth, 1966: fig. 306 m ), and the bronzed elytra with transversely stretched isodiametric microsculp-


Fig. 33. Mexican distributional records for Agonum placidum.
ture. The Mexican specimen agrees with specimens from western North America by the piceous upper body surface. Lindroth (1966) describes variation among northern North American populations.

Male aedeagal median lobe with weak wrinkles euventrally, lobe straight in apical half (Lindroth, 1966: fig. 307g).

Female reproductive tract with very elongate spermathecal duct, about $6 \times$ length of fusiform apical reservoir; basal gonocoxite with apical fringe of about seven setae; apical gonocoxite with two lateral and one dorsal ensiform setae.

Distribution. Transamerican from Nova Scotia to Alaska (Lindroth, 1966), south to Maryland (MCZ) in the east, and California in the west. California localities include Shotgun Lake, Nevada Co. (CAS), and E of Quincy, Plumas Co. (CISC, CUIC). The population pesent near Mexico City during the collecting phase of the "Biologia" is the only one discovered in Mexico (Fig. 33).

Mexican material. [Distrito Federal]: Mexico [City] (BMNH, 1).
Ecology. On the edges of open marshes and wet meadows with standing water. It prefers firm soil, and plant cover such as Carex and mosses (Lindroth, 1966). In Plumas Co., CA, it was found at $1,000 \mathrm{~m}$ elevation in a wet cow pasture. Beetles were found along the water's edge, and under logs on damp soil in the shade of trees. A. suturale was also collected at this spot, suggesting the species might be found together in Mexico.


Fig. 34. Mexican distributional records for Agonum propinquum ( $\boldsymbol{\wedge}$ ), A. suturale $(\boldsymbol{\ominus})$, and A. pacificum (■).

## placidum species group (subgenus Paragonum Casey, 1920; type placidum Say)

Species group diagnosis. Neck shortened, not constricted or elongate (^); pronotal lateral margins straight before hind angles ( ${ }^{\wedge}$ ); pronotal hind angles with minute jag ${ }^{*}$ ); elytra with 4-8 dorsal punctures in or adjacent to third interval (except the Palaearctic $A$. numidicum Lucas) ( ${ }^{\wedge}$ ); dorsal body surface metallic, on elytra metallic sheen restricted to margins or found across elytral surface ( ${ }^{\wedge}$ ).

## Agonum placidum Say

Feronia placida Say, 1823:43.
Agonum alcyoneum Chaudoir, 1837:24.
Agonum morosum Dejean, 1828:145.
Agonum amplior Casey, 1920:124.
Agonum aztecanum Casey, 1920:124.
Agonum citatum Casey, 1920:124.
Agonum rhodeanum Casey, 1924:84.
Types. Of placida, neotype $\&$ (Lindroth and Freitag, 1969), Dorchester, MA (MCZ); of alcyoneum, lectotype $\widehat{o}$ (Liebherr, 1991a), Mexico City (MNHP); of morosum,
lectotype ô (Lindroth, 1955), "Amér. sept." (MNHP); of amplior, lectotype $q$ (Lindroth, 1975), Boudler, CO (NMNH); of aztecanum, lectotype $q$ (Lindroth, 1975); Amecameca, Mexico (NMNH); of citatum, lectotype ô (Lindroth, 1975), New Hampshire (NMNH); of rhodeanum, lectotype ồ (Lindroth, 1975), Rhode Island (NMNH).

Diagnosis. Agreeing with species of the cyclifer species group by the granulate isodiametric elytral microsculpture and blue metallic sheen on pronotal base and elytra, but with basal pronotal margin not expanded posteriorly behind laterobasal depressions, and pronotal basal angles evident, lateral margin straight to slightly concave just before basal seta (Lindroth, 1966: figs. 309, 310a). Also differing by the trisetose metacoxae (bisetose in cyclifer group). Body length $6.8-8.8 \mathrm{~mm}$.

Male aedeagal median lobe evenly curved in apical half, euventral surface smooth, apex blunt (Fig. 24).

Female reproductive tract with moderately elongate spermathecal duct, about 5$6 \times$ length of apical reservoir; basal gonocoxite with apical fringe of about eight setae; apical gonocoxite with two lateral ensiform setae; single dorsal ensiform seta on mesal surface, exposed in ventral view (Liebherr, 1986: fig. 6g).

Distribution. Broadly Transamerican in distribution, but not reaching the Pacific Coast (Lindroth, 1966). The westernmost known locality is the Eureka Valley, Inyo Co., CA (D. Giuliani coll., CDFA). This species has been collected at a number of localities in southeastern Arizona. In Mexico, it is found along the eastern slopes of the Sierra Madre Occidental, in the Sierra Madre Oriental, and south to the Transvolcanic Sierra, Valley de Oaxaca, and Sierra de Miahuatlán of Oaxaca (Fig. 34).

Mexican material. MÉXICO. [no other data] (BMNH, 1; CAS, 37); San Antonio de Arriba (BMNH, 3). Aguascalientes: Ridge NW Presa Jocoqui (CAS, 10). Chihuahua: Catarinas, $6,100 \mathrm{ft}$ (CAS, 1); Colonia Garcia, 2,130 m, meadow \& adj. pineoak for. (UASM, 2), $13.2 \mathrm{~km} \mathrm{~N}, 1,900 \mathrm{~m}$, meadow nr. creek (UASM, 3); Ejido Zaragoza, i5.2 km N, $2,150 \mathrm{~m}$, meadow (UASM, 6); Hidalgo del Parral, 5,500 ft (UCDC, 1); Madera (CAS, 1), $48.1 \mathrm{~km} \mathrm{N}, \mathrm{2,480} \mathrm{m}, \mathrm{oak-pine} \mathrm{forest} ,\mathrm{litter} \mathrm{(UASM}$, 5), 6.5 mi W, 2,320 m (UASM, 2); Matachic (AMNH, 1); Mesa del Huracán (CNC, 1), $7,400 \mathrm{ft}$ (CNC, 1); Miñaca, $31.9 \mathrm{mi} \mathrm{S}, 8,100 \mathrm{ft}$ (UASM, 1). Coahuila: San Antonio de las Alazanos, 6 mi E, $7,900 \mathrm{ft}$ (UASM, 1); Viesca, 8 mi N, Bilbao dunes, 3,200 ft, UV light (CUIC, 1). Distrito Federal: creek at Lomas de Chapultepec (MCZ, 3), H. Chapultepec (MCZ, 2); La Venta (CAS, 4); Mexico City (BMNH, 2; NMNH, 1); México, 29 km S on Rte. 3, 8,600 ft, damp agric. area (MCZ, 1); San Jeronimo (AMNH, 1); Tulyehualco (CNC, 2). Durango: Cueva, 8,850 ft (MSUC, 1); Durango (NMNH, 5), 27.5 mi W, Rte. 40, 7,600 ft, creek margin (UASM, 3), $5 \mathrm{mi} \mathrm{W}, 6,500$ $\mathrm{ft}(\mathrm{CNC}, 2)$; El Salto, $10 \mathrm{mi} \mathrm{W}, 9,000 \mathrm{ft}(\mathrm{CNC}, 1), 26 \mathrm{mi} \mathrm{E}, 8,700 \mathrm{ft}(\mathrm{MCZ}, 2)$; Graceros (MSUC, 5); Hidalgo del Parral (Chih.), $86.5 \mathrm{~km} \mathrm{~S}, 1,750 \mathrm{~m}$, pasture, UV light (UASM, 3); Tapias (MSUC, 1). Hidalgo: Apam, 0.8 km N (NMNH, 2); Pachuca (CAS, 1), acacia grove (UASM, 18); Real del Monte (Pachuca) (BMNH, 1); Tizayuca, 5 mi N (CAS, 1). Jalisco-Zacatecas: Huejuquilla el Alto (Jal.), 25.6 km W , rd. to San Juan Capistrano, 1,050 m, cactus \& acacia, UV light (UASM, 4). México: Agua Bendita, 10 km N, W Toluca, $9,000 \mathrm{ft}$, slope, pasture (UASM, 1); Amecameca (CAS, 3; MCZ, 1; NMNH, 1), 7 km S, Rte. 115 (UASM, 11); El Yukón, Rte. 15, W Toluca, 8,800 ft (UASM, 2); La Hortaliza, 27 mi W (UASM, 6); Lerma, 4 km E, Rte. 15, 9,000 ft (UASM, 3); Parc Nac. Bosencheve, 2,700 m (DmMC, 3); Temascaltepec (CAS, 5), Real de Arriba (MCZ, 1), Tejupilco, $4,000 \mathrm{ft}$ (BMNH, 1); Tepetlixpa, 10.5
km S Amecameca, Rte. 115, 2,200 m, pine-oak hillside (CUIC, 2); Toluca (BMNH, 2), 18 km SW , Rte. 130, $3,460 \mathrm{~m}$, meadow (UASM, 1), $9.1 \mathrm{mi} \mathrm{SW}, \mathrm{9,600} \mathrm{ft} \mathrm{(UASM}$, 25). Michoacán: (CAS, 1); Angahuán, 1.1 mi E, $7,300 \mathrm{ft}$, cornfield, edge of lava flow (UASM, 20); Atlamimicán, 3 km NE Contepec, 2,600-3,230 m (CMNH, 1); Carapan, 11 mi S, $6,990 \mathrm{ft}$ (UASM, 4); Cerro de Capatzun, nr. Angahuán, 73-7,500 ft (UASM, 1); Cheran, 4.9 km N , Rte. $37,2,127 \mathrm{~m}$, under stones, fields (UASM, 2); Ciudad Hidalgo, 24.9 mi W, Rte. $15,8,760 \mathrm{ft}$, cornfield (UASM, 1); Huajúmbaro, Rte. 15 , $8,500 \mathrm{ft}$, pasture (UASM, 2); Peribán de Ramos, 35.4 km E, $2,150 \mathrm{~m}$, under wood, edge cult. field (UASM, 1); Uruapan, $56.3 \mathrm{~km} \mathrm{~N}, 2,050 \mathrm{~m}$, grownover field (UASM, 1). Morelos: Cuernavaca, 9 mi N, $8,500 \mathrm{ft}$ (CUIC, 6); El Guardia (UASM, 1). Nuevo Leon: Galeana, 4 mi SW, Lago La Laguna, 5,600 ft (CUIC, 1), Cerro Potosí, 2,347 m, scrub oak litter (UASM, 1). Oaxaca: Santa Ines del Monte to Cuatro Venados, $9,000 \mathrm{ft}(\mathrm{UASM}, 1)$; microondas, 0.5 mi E jct. Rtes. $190 \& 125,2,529 \mathrm{~m}$ (UASM, 5), 2,650 m, oak forest (dry) (UASM, 4), 8,300 ft, oak forest (UASM, 9); Pacific slope, rd. between Oaxaca and Puerto Angel, 5,000 ft (NMNH, 1); Puebla: Azumbilla, $50.8 \mathrm{~km} \mathrm{SE}, 2,480 \mathrm{~m}$, oak-pine forest, ground (UASM, 1); San Andres Chalchicomula [=Ciudad Serdan] (BMNH, 1); Santa Maria del Monte V. G., 7.6 km E, 2,480 m, fallow fields (UASM, 2), 2,640 m, oak-pine forest (UASM, 3); Tlachichuca, $8,300 \mathrm{ft}$ (UASM, 35), 3 mi E, $8,600 \mathrm{ft}$ (UASM, 24); Zacatepec, 6 km NE, 2,450 m (CUIC, 3), 7.7 km NE, $2,390 \mathrm{~m}$, oak-pine, rocky litter (UASM, 6). Queretaro: Palmillas, nr., $7,000 \mathrm{ft}$, pond \& environs (UASM, 1); Pinal de Amoles, 9.4 km SW, Rte. 120, 2,450 m, oak-pine edge cultivation (UASM, 5). San Luis Potosí: Matehuala, 8 mi E, on hill, desert scrub (CUIC, 2). Sonora: Sierra Huachinera, 23.4 km SE Huachinera, $2,090 \mathrm{~m}$, meadow, pine-oak for. (UASM, 4). Tamaulipas: Palmillas, 51.8 km N , $2,680 \mathrm{~m}$, pine w/oak, ridgetop under $\log$ (UASM, 1). Tlaxcala: Apizaco, 2 mi SE, 1.2 mi S. Rte. 136 toward Teacalco (OHSC, 2); Malinche Nat. Pk., Matlalcueyetl, NE slope; 3.9 km Los Pilares, $2,900 \mathrm{~m}$ (UASM, 9); Teacalco, 1.2 mi S , jct. rte. 136 (OHSC, 2), 8,500 ft, conifer forest (OHSC, 1); Tlaxco, 6.8 km N, Llano Tiopa, 2,820 m, meadow, fir forest (UASM, 6). Veracruz: Cuidad Mendoza, 13.2 mi W, Rte. 150D, 6,600 ft (UASM, 5); Cuiyachapa, 15.3 km W Coscomatepec, $2,520 \mathrm{~m}$, pasture (UASM, 4); Jalapa (AMNH, 1); Las Vigas (AMNH, 6; BMNH, 36; MCZ, 12; NMNH, 12); Perote, 2 km E, 2,900 m (CUIC, 16).

Ecology. This species is found in drier habitats than many other species of the genus. Habitats range from 1,050-3,460 m elevation in Mexico, and include cactus and acacia scrub, pine-oak forest, fallow fields, and in one case, a cornfield at the edge of a lava flow. It has also been found on the margins of ponds in open soil. On Cerro Perote, Veracruz state, a large series was found on slightly damp soil under pines in open forest with agave and cactus. These were microsympatric with small species of the tenebrionid genus Eleodes.

## belleri species group

(subgenus Punctagonum Gray, 1937; type belleri Hatch)
Species group diagnosis. Neck shortened, not constricted or elongate ( ${ }^{\wedge}$ ); upper body surface vividly metallic (except $A$. fossigerum) (^); legs and epipleura dark, concolorous with ventral body surface (except A. fallianum) $\left(^{*}\right.$ ); profemur with 2-3 anteroventral setae and 4-5 posterior setae ( ${ }^{\wedge}$ ); mesofemur with 3-6 anteroventral
setae ( ${ }^{\wedge}$ ); metacoxae bisetose ( ${ }^{\wedge}$ ); metafemur with 3 anteroventral setae ( ${ }^{\wedge}$ ); median lobe of aedeagus straight or recurved in apical half (except for A. muiri which is more evenly arcuate) (*).

## Agonum suturale Say

Agonum suturale Say, 1830:[3] (see Bousquet, 1993).
Platynus subsericeus LeConte, 1863:8 (NEW SYNONYMY).
Agonum viridissimum Casey, 1920:103.
Agonum suffusum Casey, 1920:104.
Agonum suffusum latiusculum Casey, 1920:104.
Agonum suffusum uteanum Casey, 1920:104.
Agonum sierranum Casey, 1920:105.
Agonum sierranum sequioarum Casey, 1920:105.
Agonum sybariticum Casey, 1920:107.
Types. Of suturale, original type series destroyed, neotype ${ }^{\text {on }}$ "MEX. Tlaxcala, 6.8 km. n. Tlaxco, 2820 n . Llano Tiopa, meadow \& fir forest, June 29-30, 1975/MEX. EXP. 1975, G. E. Ball \& H. E. Frania collectors" (UASM, deposited in MCZ), hereby designated; of subsericeus, lectotype $q$ (Lindroth, 1966), Kansas (CMNH); of viridissimum, lectotype ô (Lindroth, 1975), Stockton, UT (NMNH); of suffusum, lectotype $\$$ (Lindroth, 1975), Agassiz, BC (NMNH); of latiusculum, lectotype 9 (Lindroth, 1975), California (NMNH); of uteanum, lectotype $\ddagger$ (Lindroth, 1975), Ogden, UT (NMNH); of sierranum, lectotype $\%$ (Liebherr, 1991a), Truckee, CA (NMNH); of sequoiarum, holotype $\%$ (Liebherr, 1991a), Redwood Creek, CA (NMNH); of sybariticum, lectotype $\%$ (Liebherr, 1991a), Lake Henshaw, CA (NMNH).

Diagnosis. Mexican specimens are brilliant metallic green, blue-green, or bronze with green elytral margins. Pronotum with rugose laterobasal depressions, wrinkles sometimes well developed on disc (Fig. 12); hind angles evident, marginal bead continuous at basal setae, obsolete medially. Elytral intervals flat; third interval uniformly with three dorsal setae in Mexican specimens. Abdominal and thoracic sternites piceous, legs concolorous to slightly paler; metepisternum and elytral epipleura metallic. Body length $8.5-11.0 \mathrm{~mm}$.

Male aedeagal median lobe wrinkled euventrally (Fig. 25); apical half straight, apex acuminate; median lobe bilaterally constricted, narrow apically in euventral view.

Female reproductive tract with very elongate spermathecal duct, about $9-10 \times$ as long as apical reservoir, duct repeatedly coiled near base of reservoir; basal gonocoxite with apical fringe of 11-12 setae; apical gonocoxite with two to three lateral and one dorsal ensiform setae.

Distribution. Found in the western half of North America, from Alberta and Saskatchewan, south along the Rocky Mountain, Cascade, and Sierra Nevada Ranges, and east to Kansas (Lindroth, 1966). In Mexico, it occurs in the Sierra Madre Occidental and Transvolcanic Sierra (Fig. 33).

Mexican material. Aguascalientes: El Retoño, 10 mi E Aguascalientes (AMNH, 2). Chihuahua: Guerrero (USNM, 1); Madera, 5.5 mi W, $2,270 \mathrm{~m}$, lake margin (UASM, 14). Durango: El Salto, Cruz de Piedra, 2,350 m (DmMC, 3), 6 mi NE, $8,500 \mathrm{ft}(\mathrm{AMNH}, 1)$; Otinapa, $7,500 \mathrm{ft}$ (AMNH, 4), 8,200 ft (AMNH, 1). México:


Figs. 35, 36. Agonum pacificum. 35. Right half of pronotum. 36. Median lobe of male aedeagus, internal sac inverted, dorsal view.

Atlacomulco, 2,500 m (UMMZ, 1); Toluca (BMNH, 3). Tlaxcala: Tlaxco, 6.8 km N , Llano Tiopa, $2,820 \mathrm{~m}$, meadow \& fir forest (UASM, 1).

Ecology. In Mexico, this species has been found in habitats from 2,270-2,800 m. These include lake margins, and fir forest and meadows at higher elevations. Lindroth (1966) states that this species is markedly hygrophilous.

## Agonum pacificum Casey

Agonum pacificum Casey, 1920:102.
Type. Lectotype ô (Liebherr, 1984), Julian, CA (NMNH).
Diagnosis. Pronotum with evident hind angles, nearly continuous basal marginal bead and minutely punctured laterobasal depressions (Fig. 35). Elytral intervals slightly convex; five to six setae in or adjacent to third interval. Upper body surface shiny bronze; elytra with isodiametric sculpticells in irregular transverse rows. Body length $8.2-11.0 \mathrm{~mm}$.

Male aedeagal median lobe wrinkled euventrally (Fig. 36); euventral surface recurved in apical half, apex inflexed relative to median bulge; parameres and median lobe near parameral articulation darker than lobe apex.

Female reproductive tract with elongate spermathecal duct, $4-5 \times$ as long as apical reservoir; basal gonocoxite with apical fringe of about 10 setae; apical gonocoxite with three lateral and one dorsal ensiform setae.

Distribution. Found in the Coast Range of California from the San Francisco Bay Area south to San Diego, and in the Tehachapi Pass region of the southern Sierra Nevada (Liebherr, 1984). In Mexico, it is restricted to the Sierra de San Pedro Martir of northern Baja California (Fig. 33).


Figs. 37-42. Aedeagal median lobe with internal sac distended, ventral view. All to same scale. 37. Agonum cyanope. 38. A. extimum. 39. A. parextimum. 40. A. texanum. 41. A. extensicolle. 42. A. decorum.


Fig. 43. Mexican distributional records for Agonum cyanope.

Mexican material. Baja California Norte: Sierra San Pedro Martir, La Grulla, $6,900 \mathrm{ft}(\mathrm{CAS}, 4)$, Lower La Grulla meadow (CAS, 1), Rancho Viejo N of La Grulla (CAS, 1).

Ecology. In northern California, I have collected this species along creek margins on damp soil in open oak woodland.

## extensicolle species group

Species group diagnosis. Antennal scape with $>3$ apical setae (*), pedicel with apical ring of setae $\left(^{*}\right)$; elytral striae weakly punctate ( ${ }^{\wedge}$ ); elytra with 4-8 dorsal setae $\left(^{\wedge}\right.$ ); upper body surface metallic, at least on head and elytra ( ${ }^{\wedge}$ ); pronotum with isodiametric microsculpture $\left({ }^{*}\right)$, elytra with isodiametric granulate microsculpture $\left(^{*}\right)$; profemur with 4-8 posterior setae ( ${ }^{\wedge}$ ); mesocoxa with $2-4$ ridge setae ( ${ }^{\wedge}$ ); mesofemur with 3-6 anteroventral setae ( ${ }^{\wedge}$ ); metacoxa bisetose ( ${ }^{\wedge}$ ); metafemur 3-4 anteroventral setae ( ${ }^{\wedge}$ ); metatarsi with dorsal surface medially carinate $\left(^{*}\right)$.

## Agonum cyanope Bates

Anchomenus cyanopis Bates, 1882:94.
Type. Lectotype ô (Liebherr, 1982), Guanajuato, Mexico (BMNH).


Fig. 44. Mexican distributional records for Agonum extimum ( $\odot$ ) and A. parextimum $(\diamond)$.

Diagnosis. Upper body surface piceous with blue to purple metallic sheen. Pronotum with evident hind angles, lateral margins straight to slightly convex before basal setae (Fig. 13); laterobasal depressions punctate. Body length 7.1-9.2 mm.

Male aedeagal median lobe with (Fig. 37) or without euventral wrinkles; lobe straight in apical half, apex finely rounded.

Female reproductive tract with spermathecal gland duct entering medially on elongate spermathecal duct (Liebherr, 1986: fig. 38c); spermathecal apical reservoir with 24-30 beadlike constrictions along length.

Distribution. Found in the Cochise filter/barrier region of southeastern Arizona and southwestern New Mexico (Liebherr, 1986), and in the Sierra Madre Occidental and Transvolcanic Sierra of Mexico (Fig. 43).

Mexican material. Chihuahua: Babícora San José (AMNH, 4); Bachiniva (UAZC, 1); Caborachic, $9.8 \mathrm{~km} \mathrm{~W}, 2,400 \mathrm{~m}$, pine forest, ridge top (UASM, 1); Catarinas, $5,800 \mathrm{ft}$ (AMNH, 6); Colonia Garcia, $13.2 \mathrm{~km} \mathrm{~N}, 1,900 \mathrm{~m}$, meadow near creek (UASM, 1); Ejido Zaragoza, $1.3 \mathrm{~km} \mathrm{~N}, 1,850 \mathrm{~m}$, oak-pine forest in canyon c/w creek (UASM, 1); Guerrero, Río Papagochic (NMNH, 4); Madera, 5.5 mi W, 2,270 m, lake margin (UASM, 19); Primavera, 5,500-6,000 ft (AMNH, 1); San Pablo Balleza, 31 km SE, $2,050 \mathrm{~m}$, grassland; oak-acacia (UASM, 1); Santa Barbara, 7,000-8,000 ft (AMNH, 1). Distrito Federal: Cuajimalpa (NMNH, 5); Guadelupe Hidalgo [=Gustavo A. Madero] (MCZ, 7); Mexico City (BMNH, 2). Durango: Coyotes, 8 mi N,

7,500 ft (CAS, 10); Durango (BMNH, 7; MCZ, 4; NMNH, 1), 6,200 ft (AMNH, 1), 15 mi W (CNC, 5), 65-70 km SSW road to La Flor, 2,590 m (CAS, 1); El Salto, $8,800 \mathrm{ft}(\mathrm{MCZ}, 15), 10 \mathrm{mi}$ W (CNC, 2), 9,000 ft (CNC, 41); La Ciudad (BMNH, 3), 2,570 m, meadow nr. pine-oak forest (UASM, 6); Los Altares, Santiago Papasquiaro, 2,510 m (MNHP, 10); Otinapa, 8,200 ft (AMNH, 3); Reserva de la Biosfera, La Michilia, Río Temescal, 2,400 m, creek margin, sand, rocks (UASM, 1), Trampa Las Casas, $2,500 \mathrm{~m}$, pond margin (UASM, 2), Trampa Piedra Herrada, 2,500 m, meadow \& pond edge (UASM, 2), 5 km S Trampa Las Casas, 2,500 m (UASM, 1), Mesa del Burro, Laguna del Burro, $2,700 \mathrm{~m}$, dry pond (UASM, 2). Guanajuato: Guanajuato (BMNH, 1), 14 mi NE, $7,700 \mathrm{ft}$ (UASM, 1); San Luis de la Paz, 36 mi S, Rte. 57, 2,060 m (UASM, 11). Guerrero: Amula, 6,000 ft (BMNH, 1). Hidalgo: Metzquititlán, 8.2 km N, Rte. 105, 2,500 m, cactus scrub, pedregal (UASM, 4); Tula de Allende (BMNH, 1). Jalisco: Ameca, 2 mi W hwy. jct. (AMNH, 1); Ojuelos de Jalisco, 12 mi W, 20-XI-1948 (CAS, 2). México: Atlacomulco, 2,500 m (UMMZ, 1); Temascaltepec (MCZ, 3); Tepotzotlán (UASM, 1). Morelos: Cuernavaca (BMNH, 2). Nayarit: Santa Teresa, 2,073 m (CAS, 2). Oaxaca: Microondas, 0.5 mi E jct. Rtes. $190 \& 125,2,529 \mathrm{~m}$ (UASM, 1), $8,300 \mathrm{ft}$, oak forest (UASM, 12). Puebla: Puebla (BMNH, 1; CAS, 1); Tlaxco (Tlaxcala), 28 km N, Rte. 119, 2,300 m, wet pasture (UASM, 9). San Luis Potosí: San Luis Potosí (AMNH, 4). Sonora: San Nicolas, E, rd. to La Angostura, 1,400 m, grassland-oak forest (UASM, 3); Yecora, 7,000 ft (CNC, 2). Veracruz: Jalapa (NMNH, 2). Zacatecas: Huejuquilla el Alto (Jal.), 46 km W, rd. to Jesus Maria (Nay.), $1,210 \mathrm{~m}$, arroyo, litter, nr. stream margin (UASM, 1); Tlaltenango, 32.1 km W jct. Rte. 54 and rd. to, $2,380 \mathrm{~m}$, oak-pine clearing (UASM, 2).

Ecology. Found from 1,200-2,700 m elevation, usually near water. Habitats include lake and creek margins, often in mesic wooded canyons, clearings in pine-oak forest, and wet pastures.

## Agonum extimum Liebherr

Agonum extimum Liebherr, 1986:100.
Type. Holotype $9,31.2 \mathrm{~km}$ E San Pedro de las Colonias, Coahuila, Mexico (CISC). Diagnosis. Both ventral and dorsal body surface covered with pelage of microsetae. Pronotum cordate (Fig. 14), lateral margins sinuate before hind angles; laterobasal depressions smooth. Elytra with $7-16$ setae in or adjacent to third interval. Body length $8.1-10.9 \mathrm{~mm}$.
Male aedeagal median lobe smooth euventrally, straight in apical half (Fig. 38); acuminate apex downturned.

Female reproductive tract with spermathecal gland duct entering medially on elongate spermathecal duct (Liebherr, 1986: fig. 39c); spermathecal apical reservoir with 37-40 beadlike constrictions along length.

Distribution. Found in the Chihuahuan Desert, from central Texas and Coahuila, west to the eastern slopes of the Sierra Madre Occidental and the Cochise filter/ barrier in southeastern Arizona (Liebherr, 1986). In Mexico, restricted to the Chihuahuan Desert (Fig. 44).

Mexican material. Chihuahua: Camargo, 20 mi SW, 4,500 ft (AMNH, 2), 25 mi SW (AMNH, 1), $42 \mathrm{mi} \mathrm{SW}, 4,900 \mathrm{ft}$ (AMNH, 1); Chihuahua (UASM, 1), 110 mi N (UCRC, 1); Hidalgo del Parral, 40 mi NE, Rte. $45,5,200 \mathrm{ft}$, UV light (UASM, 1);

Jiménez, 10 mi W (AMNH, 2); Parrita, 5 mi W , Cañon Santa Clara (CISC, 1); Samalayuca (AMNH, 1). Coahuila: Hermanas, 12 mi N (UCDC,1); San Pedro de las Colonias, 18.3 mi S [sic E], Rte. 40, 1,080 m (UASM, 10), 31.2 km E, Rte. 40, 900 m (CISC, 25; CUIC, 96).

Ecology. Found at lower elevations, 900-1,600 m, near desert water sources. Large numbers were found on a drying muddy creek bed on the south shore of Bolson Mapimi (CISC, CUIC). A. texanum was also found at this site.

## Agonum parextimum Liebherr

Agonum parextimum Liebherr, 1986:103.
Type. Holotype $\%$, Los Mochis, Sinaloa, Mexico (CAS).
Diagnosis. Pronotum cordate with smooth laterobasal depressions (Fig. 15) as in A. extimum, but body surface glabrous, lacking pelage of microsetae. Elytra with four to six setae in or adjacent to third interval. Body length $8.0-10.1 \mathrm{~mm}$.

Male aedeagal median lobe smooth euventrally, straight in apical half (Fig. 39), apex acuminate.

Female reproductive tract as in $A$. extimum, but with $37-47$ beadlike constrictions along spermathecal apical reservoir.

Distribution. Found in the Sonoran Desert west of the Cochise filter/barrier in southeastern Arizona (Liebherr, 1986), and along the coast of the Gulf of California in Sonora and Sinaloa (Fig. 44).

Mexican material. Sinaloa: El Venadillo (CAS, 5); Escuinapa, lights (CDFA, 1); Los Mochis (CAS, 9; UVMC, 5); Mazatlán (AMNH, 1). Sonora: Guaymas (CDFA, 1), 18 mi S (NMNH, 1); Hermosillo (CAS, 1), 40 mi (CAS, 3); Navojoa (NMNH, 2); Puerto Peñasco (AMNH, 1); Santa Ana, 10 mi N (CAS, 3), 19.8 km W, Rte. 2, Sonoran Desert, 710 m , UV light (UASM, 1).

Ecology. Presumably found in situations similar to A. extimum; desert water sources.

## Agonum texanum LeConte

Playtnus texanus LeConte, 1878:374.
Anchomenus megillus Bates, 1891:252.
Types. Of texanus, holotype ${ }^{\text {\& }}$, Clifton, TX (MCZ); of megillus, lectotype ô (Liebherr, 1982), Villa Lerdo, Mexico (BMNH).

Diagnosis. Pronotum broad with rounded hind angles, laterobasal depressions wrinkled, at most finely punctate (Fig. 16). Elytra broad, more or less flattened on disc. Body length $7.1-10.1 \mathrm{~mm}$.

Male aedeagal median lobe wrinkled euventrally, straight in apical half, apex not at all downturned (Fig. 40); aedeagal internal sac with well-developed lateral sclerites at base.

Female reproductive tract with very elongate spermathecal duct, about $9 \times$ length of fusiform apical reservoir; spermathecal gland duct entering at base of apical reservoir (Liebherr, 1986: fig. 42a).

Distribution. Ranges from Kansas southward to coastal Tamaulipas, and southwestward to Arizona south of the Rocky Mountains and Mogollon Rim (Liebherr, 1986). In Mexico, this species is found in states bordering the Rio Grande Valley,


Fig. 45. Mexican distributional records for Agonum texanum.
and in northern Sonora (Fig. 45). As in A. punctiforme, a disjunct population occurs in the highlands of Chiapas, near San Cristobal.

Mexican material. Chiapas: Comitán, 5 km E (UASM, 21). Chihuahua: Camargo, 42 mi SW (AMNH, 4); Chihuahua City (BMNH, 2; UASM, 2), 12 mi N (CAS, 2); Delicias, 4,150 ft (AMNH, 1); Escalón, 12 mi N (NMNH, 1); Hidalgo del Parral, 32 mi S (CAS, 4), 40 mi NE, Rte. 45, 5,200 ft (UASM, 3); Jiménez (NMNH, 1), 10 mi N (AMNH, 7); Primavera, 5,500-6,000 ft (AMNH, 1); Salaices (AMNH, 1); Samalayuca (AMNH, 1); Sombreretillo (CAS, 1); Valle de Olivos, 5,500 ft (AMNH, 1). Coahuila: Sabinas, 67 km S , Rte. 57, 470 m (UASM, 2); San Pedro de las Colonias, 19.5 mi E, 2,950 ft (CISC, 1; CUIC, 8); 18.3 mi E, $1,080 \mathrm{~m}$ (UASM, 1); Torreón (CAS, 2). Durango: Hidalgo del Parral (Chihuahua), $86.5 \mathrm{~km} \mathrm{~S}, 1,750 \mathrm{~m}$, pasture, UV light (UASM, 1); Villa Lerdo (BMNH, 8; NMNH, 3). Sonora: Moctezuma, 17 km SW (SMcC, 1); Sierra San Luis, Varela Rch., Cañon Bonita, $1,350 \mathrm{~m}$, UV light (UASM, 1). Tamaulipas: Ciudad Mante, 100 ft (AMNH, 1); La Pesca, 7.5 mi W, Lago Almagre (UASM, 1); Magiscatzin [=González], 13 km E (MCZ, 1); San Fernando, 29 mi N , Rte. 97, 300 ft (UASM, 1).
Ecology. Occurring from sea level to $1,700 \mathrm{~m}$ elevation, in creek bottoms, or pastures.


Fig. 46. Mexican distributional records for Agonum extensicolle.

Agonum extensicolle Say
Feronia extensicolle Say, 1823:54.
Feronia proxima Harris, 1828:132.
Anchomenus obscuratus Chaudoir, 1843:763.
Anchomenus viridis LeConte, 1848:222.
Anchomenus cyanescens Motschulsky, 1859:159.
Anchomenus gaudens Casey, 1920:55.
Anchomenus gaudens clientulus Casey, 1920:55.
Anchomenus vigilans Casey, 1920:56.
Types. Of extensicolle, neotype 9 (Lindroth and Freitag, 1969), Rumney, NH (MCZ); of proximus, original type series lost, no type locality given; of obscuratus, possible type $\%$, "Amer. sept." (MNHP); of viridis, type $\%$, Ohio River, Indiana (MCZ); of cyanescens, type $\uparrow$, California (?) (MSUM); of gaudens, lectotype $\begin{gathered}\text { (Lindroth, 1975), }\end{gathered}$ Lake Champlain, NY (NMNH); of clientulus, lectotype ð (Lindroth, 1975), New Jersey (NMNH); of vigilans, holotype $\widehat{\text { or }}$ (Lindroth, 1975), North Carolina (NMNH).

Diagnosis. Pronotum subcordate, lateral margins nearly as sinuate as in A. extimum and $A$. parextimum, but laterobasal depressions and median base rugosely punctate (Fig. 17). Upper body surface royal blue in Mexican specimens, elytra with granulate
isodiametric sculpticells purple, areas between sculpticells blue. Body length 7.110.8 mm .

Male aedeagal median lobe wrinkled euventrally, straight (Fig. 41) to evenly arcuate (Liebherr, 1986: figs. $49 \mathrm{~d}-\mathrm{g}$ ) in apical half.

Female reproductive tract with elongate spermathecal duct, about $6 \times$ length of fusiform apical reservoir; gland duct entering at base of apical reservoir (Liebherr, 1986: fig. 45a).

Distribution. Broadly distributed across eastern North America from Nova Scotia to Lake Winnipeg and central Montana, southward to the Cochise filter/barrier of Arizona (Liebherr, 1986). In Mexico, this species is restricted to the eastern slopes of the Sierra Madre Occidental and the northern slopes of the Transvolcanic Sierra (Fig. 46).

Mexican material. Aguascalientes: Aguascalientes, 11 mi W, Rte. $70,5,500 \mathrm{ft}$ (UASM, 1), $5.3 \mathrm{mi} \mathrm{N}, 6,100 \mathrm{ft}$ (UASM, 14). Chihuahua: Casas Grandes (MCZ, 1); Chihuahua City (BMNH, 5; NMNH, 1); Colonia Garcia, 2,130 m, meadow \& adj. pine-oak forest (UASM, 2), 13.2 km N, $1,900 \mathrm{~m}$, meadow near creek (UASM, 1), $4.8 \mathrm{~km} \mathrm{~S}, 2,130 \mathrm{~m}$, pine-oak-madrino, ravine (UASM, 1); Ejido Zaragoza, 1.3 km $\mathrm{E}, 1,800 \mathrm{~m}$, creek edge (UASM, 6), $1.3 \mathrm{~km} \mathrm{~N}, 1,850 \mathrm{~m}$, oak-pine forest in canyon creek (UASM, 19); Madera, 7,200 ft (AMNH, 1); Mesa de Tres Ríos (Sonora), 48.8 km E, 1,790 m, stream margin (UASM, 1); Miñaca, $20.1 \mathrm{mi} \mathrm{S}, 6,700 \mathrm{ft}$ (UASM, 1); Primavera, 5,500-6,000 ft (AMNH, 5); Primavera vic., Cañon Prieta (ANMH, 2); San Pablo Balleza, 4.2 km W, 1,640 m, creek edge, gravel, sand, clay (UASM, 5); Santa Clara (AMNH, 1), Namiquipa Dist., 6,500 ft (AMNH, 1). Durango: Durango, 16 mi NW, Río Chico, Rte. 40, 6,500 ft (UASM, 19); El Banco, $12.2 \mathrm{mi} \mathrm{S}, 5,220 \mathrm{ft}$ (UASM, 6), $27.5 \mathrm{mi} \mathrm{S}, 7,600 \mathrm{ft}$ (UASM, 3); Graceros, 6,000 ft (MSUC, 10); Reserva de la Biosfera, La Michilia, Trampa Piedra Herrada, $2,500 \mathrm{~m}$, meadow \& pond edge (UASM, 1); Río Chico, 6,400 ft (MSUC, 1); Villa Lerdo (BMNH, 1); Villa Ocampo (AMNH, 1). Hidalgo: Tasquillo vic., Río Tula, Rte. 85, 5,300 ft (UASM, 1). Jalisco: Encarnación de Diaz, 9.7 mi E, Puente Caquixtle, 5,500 ft (UASM, 2). San Luis Potosí: Mexquitic, 7.5 mi NW, Rte. 49, Puente la Parada, $7,000 \mathrm{ft}$ (UASM, 1). Sonora: Mesa de Tres Ríos, 18 km N, Río Tres Ríos, $1,450 \mathrm{~m}$, stream margin (UASM, 7). Zacatecas: Fresnillo, 16 mi NW, Río Trujillo, $6,600 \mathrm{ft}$ (CAS, 1); Sain Alto, 1.3 mi SE, 6,500 ft (UASM, 2).

Ecology. This species prefers creek or pond margins with firm gravel and sand substrate, often with adjacent open oak forest. It occurs from $1,450-2,500 \mathrm{~m}$ elevation.

Flight-wing condition. Brachyptery is rarely observed in this species (2 of 137 individuals examined by Liebherr, 1986). All examined Mexican specimens proved to be macropterous.

## Agonum decorum Say

Feronia decora Say, 1823:53.
Anchomenus californicus Dejean, 1828:127.
Anchomenus thoracicus Dejean, 1828:114.
Anchomenus obscurus LeConte, 1848:223.
Platynus simplex LeConte, 1854:46.


Fig. 47. Mexican distributional records for Agonum decorum ( = green glabrous morph; $=$ green hirsute morph; $\diamond=$ red hirsute morph).

Anchomenus charmis Bates, 1884:280.
Platynus hornii Hausen, 1890:235.
Platynus testaceonotus Hausen, 1891:162.
Anchomenus solutus Casey, 1920:60.
Anchomenus impictus Casey, 1920:60.
Anchomenus irruptus Casey, 1920:60.
Anchomenus vinnulus Casey, 1920:61.
Anchomenus luxatus Casey, 1920:67.
Anchomenus decorus arenarius Casey, 1920:68.
Anchomenus tepidus Casey, 1920:68.
Anchomenus uteanus Casey, 1924:81.
Anchomenus decorus syracusensis Hatch, 1926:247.
Agonum extensicolle cubanum Darlington, 1934:97.
Types. Of decora, neotype ô (Lindroth and Freitag, 1969), Arlington, MA (MCZ); of californicus, holotype 9 (Lindroth, 1955), California (NMHP); of thoracicus, holotype $q$ (Lindroth, 1955), Utah (NMHP); of obscurus, type $\%$, Onondaga Lake, NY (MCZ); of simplex, type $\widehat{\text { or }}$, Colorado River, CA (MCZ); of charmis Bates, holotype \&, Mexico City (MNHP); of hornii, type, Canada (MCZ); of testaceonotus, holotype apparently lost; of solutus, holotype $\$$, Reno, NV (NMNH); of impictus, lectotype ô
(Liebherr, 1991a), San Joaquin Co., CA (NMNH); of irruptus, lectotype ô (Lindroth, 1975), Priest River, ID (NMNH); of vinnulus, lectotype ô (Liebherr, 1991a), Battle Mountain, NV (NMNH); of luxatus, lectotype ô (Lindroth, 1975), Utah (NMNH); of arenarius, holotype $\begin{gathered} \\ \text { (Lindroth, 1975), Galveston, TX (NMNH); of tepidus, ho- }\end{gathered}$ lotype $\$$ (Lindroth, 1975), Tucson, AZ (NMNH); of uteanus, lectotype ô (Liebherr, 1991a), Callao, UT (NMNH); of syracusensis, holotype ઠ̂, Onondaga Co., NY (ORSC); of cubanum, holotype ô, Soledad, Cienfuegos, Cuba (MCZ).

Diagnosis. Pronotum quadrate, maximum width slightly greater than median length, lateral margin sinuate before rounded hind angles (Fig. 18); laterobasal depressions sparsely punctate, basal median area not punctate. Upper body surface either with or without pelage of microsetae; prothorax either dark metallic green or ferruginous (see below).

Male aedeagal median lobe weakly wrinkled euventrally, straight (Fig. 42) to more evenly arcuate (Liebherr, 1986: figs. 50d-g) in apical half; apex slightly downturned.

Female reproductive tract with elongate spermathecal duct, about $10 \times$ length of fusiform apical reservoir; spermathecal gland duct entering at base of apical reservoir (Liebherr, 1986: fig. 50c).
Distribution. This species is Transamerican in distribution, and is found throughout the United States, southern Canada, Mexico, and on the Greater Antilles excepting Puerto Rico (Liebherr, 1986). The species is polymorphic for color (either green or red prothorax) and dorsal setosity (either glabrous or setose upper body surface) (Liebherr, 1983). The four morphs, determined by two diallelic genes, are all known from southeastern Arizona. In Mexico, the green-hirsute morph has been collected in northern Sonora, and the red-glabrous morph has been collected in western Chihuahua, suggesting that polymorphic populations occur in those states. Farther south, only the green-glabrous morph has been collected from the Pacific Coast of Sonora and Sinaloa, across the southern Sierra Madre Occidental, the Transvolcanic Sierra, and Chiapan highlands (Fig. 47).
Mexican material. All specimens are the green-glabrous form unless indicated otherwise. Baja California Norte: (FMNH, 1); Ensenada (UKSM, 2); Ojos Negros (CNC, 1), 3 mi N, at light (CAS, 1). Chiapas: Amatenango del Valle, pasture-lake (UASM, 8); Lagos des Calores, Rte. 17 (UASM, 1); San Cristobal de las Casas, 7,000 $\mathrm{ft}(\mathrm{CNC}, 2), 8.6 \mathrm{mi}$ E, Rancho Nuevo, 7,900-9,200 ft (UASM, 3). Chihuahua: Madera, 5.5 mi W [red-hirsute form], 2,270 m, lake margin (UASM, 1). Distrito Federal: Guadelupe Hidalgo [=Gustavo A. Madero] (MCZ, 12); Mexico City (BMNH, 1). Durango: Graceros, 6,000 ft (MSUC, 1); Rodeo, 8 km N, 6.4 km W, $1,417 \mathrm{~m}$, UV light (UASM, 1). Guanajuato: Lago Yuriria, nr. Yuriria, 6,500 ft (UASM, 1); Salvatierra, $5,600 \mathrm{ft}$, roadside pond (UASM, 1). Jalisco: Encarnación de Diaz, 9.7 mi E, Rte. 45, Puente Caquixtle, $5,500 \mathrm{ft}$ (UASM, 2), 21.4 mi S , Rte. $45,6,000 \mathrm{ft}$ (UASM, 4); Lago de Moreno, 13 mi SE, Rte. 45, reservoir, 6,450 ft (UASM, 1); Talpa de Allende, $4.9 \mathrm{mi} \mathrm{S}, 4,240 \mathrm{ft}$ (UASM, 2); Tecolotlán (UCDC, 2); Tomatlán, $24 \mathrm{~km} \mathrm{~S}, 61 \mathrm{~m}$, UV light (UASM, 1). México: Atlacomulco, 2,500 m (UMMZ, 2); Ayotla (MCZ, 1); El Yukón, Rte. 15, W Toluca, $8,800 \mathrm{ft}$ (UASM, 4); Toluca (BMNH, 1), 34 km W, Rte. $15,8,500 \mathrm{ft}$, creek margin (UASM, 1). Michoacán: Jiquilpan, 10.0 mi W (UASM, 2). Morelos: Morelos, Cuernavaca (MCZ, 4). Nayarit: Las Piedras, 57.9 km SW, 70 m , UV light (UASM, 1); Tepic, 3,000 ft (CMNH, 1). Nuevo Leon: Galeana, 3.0 mi W, $5,800 \mathrm{ft}$, marl pond (UASM, 5). Oaxaca: Oaxaca (BMNH, 1).

Puebla: Atlixco, 12 mi S, 4,900 ft (UKSM, 21); Puebla (BMNH, 1); Puente Ahuehueyo, 6 mi W jct. Rtes. 115 \& 190, 4,200 ft (UASM, 1); Puente Estudo, nr. Tepexco, Rte. 115, 4,000 ft (UASM, 1), black light (UASM, 1). Queretaro: Palmillas vic., 7,000 ft , pond and environs (UASM, 1). San Luis Potosí: San Luis Potosí, 18 mi S, Rte. 57, 5,300 ft (UASM, 7). Sinaloa: Escuinapa, lights (CDFA, 2); La Noria (BMNH, 2); Mazatlán, along river (BMNH, 2; MCZ, 1; NMNH, 6), UV light (NMNH, 3); Rosario (CAS, 11); Ventanas [=100 km NE Mazatlán on Río Presidio], 2,000 ft (BMNH, 2). Sonora: Ciudad Obregón, 16 mi NE (CNC, 1); Imuris, 9 mi NNE [green hirsute] (UKSM, 1). Tabasco: Ciudad Pemex, S, 175 ft, UV light (UASM, 1); San Juan Bautista [=Villahermosa] (BMNH, 2), 59.4 mi SE, black light (UASM, 2). Tamaulipas: Ciudad Mante, UV light (UASM, 2). Veracruz: Cotaxtla Exp. Sta., light trap (CNC, 1); Fortín de las Flores, UV light (UASM, 1); Jalapa (BMNH, 7; MCZ, 1). Zacatecas: Salinas del Peñón Blanca (San Luis Potosí), 23 mi SE (UASM, 1).

Ecology. Usually found along the water's edge of marshes or ponds, on organic soil with much plant cover. Habitats range in elevation from sea level to $2,700 \mathrm{~m}$ in Mexico.

## ZOOGEOGRAPHIC RELATIONSHIPS OF MEXICAN AGONUM

Relative to the overall Mexican platynine fauna, which includes nearly 300 species of Platynus, the Agonum fauna is depauperate. Of the 15 species known to occur in Mexico, 7 are widespread throughout portions of the rest of North America. These include $A$. punctiforme, $A$. placidum, $A$. suturale, $A$. propinquum, $A$. texanum, $A$. extensicolle, and $A$. decorum.

Inclusion of portions of Mexico in the ranges of these species is not based on common ecological preferences shared by these Agonum. A. punctiforme is found in lowland situations throughout the eastern United States, in the Rio Grande Valley, and along the Sinaloa coast (Fig. 26). A. extensicolle is found at lower elevations in eastern North America, where it inhabits riparian habitats along smaller streams (Liebherr, 1986). In Mexico it is found along submontane streams at elevations from $1,450-2,500 \mathrm{~m}$. A. suturale and A. propinquum are restricted to still higher elevations in Mexico, and farther north are found in montane and boreal habitats. These last two species would qualify as elements of the boreo-montane fauna described by Ball (1970). In all of these examples, tracking of similar habitats across the species range can explain Mexican distributions. An eighth species, A. pacificum, is restricted to montane habitats in California, and its occurrence in the mountains of Baja California (Fig. 33) can be similarly interpreted.

Extensive disjunctions occur in the distributions of $A$. punctiforme (Fig. 26) and A. texanum (Fig. 45), with populations isolated in the Chiapan highlands far south of other known Mexican localities. Isolation of temperate biotic elements with eastern North American affinities in the Chiapan-Guatemalan highlands occurs commonly enough in a variety of taxa to have been proposed as a general pattern (Rosen, 1978).

The remaining seven species of Agonum occurring in Mexico comprise two clades; 1) the cyclifer species group with four species, and 2) a clade within the extensicolle species group comprising $A$. cyanope, and the sister species $A$. extimum and $A$. parextimum (Liebherr, 1986). In the latter group, the two sister species are respectively restricted to the Chihuahuan and Sonoran desert regions (Fig. 44), their ranges


Fig. 48. Areas of endemism recognized for Mexico.
divided by the Sierra Madre Occidental. Sympatry is possible, but as yet undocumented, in the Cochise filter/barrier; the lowlands in southeastern Arizona adjoining these two deserts. A. cyanope is found in higher elevation habitats within the Sierra Madre Occidental and the mountains of Arizona (Fig. 43).

The four cyclifer group species vary in the amount of distributional overlap. $A$. patinale, the sister species to the other three (unpubl. data), is the most southerly distributed of the four (Fig. 27), and alone occurs south of the Isthmus of Tehuantepec, from Chiapas to Nicaragua. A. cyclifer, the sister species to the clade of $A$. anthracinum + A. scutifer, is found in the Chihuahuan desert, Rio Grande Valley and adjoining areas (Fig. 28). Except for its occurrence in southeastern Arizona, this species is allopatric with its sister group. Finally, the sister species $A$. anthracinum and $A$. scutifer broadly overlap, but differ in that the former's range (Fig. 29) surpasses the latter's (Fig. 31), with A. anthracinum found both in Arizona and south of the Rio Balsas in Guerrero and Oaxaca. The cyclifer species group is the sister to the punc-


Figs. 49-52. Taxon-area cladograms for four groups of Carabidae inhabiting the areas of endemism of Fig. 48. 49. Agonum cyclifer species group. 50. Clade of three species in the Agonum extensicolle species group. 51. Clade of three species of Notiobia, subgenus Anisotarsus (Noonan, 1973). 52. Clade of the two Mexican and Central American species of Loricera (Ball and Erwin, 1969).
tiforme species group, a group of five species found in eastern North America (unpubl. data), with A. punctiforme, as mentioned above, also found in Mexico.

In an effort to determine whether species distributions in these two clades of Agonum provide any general information on the distributional history of the Mexican biota, they were compared to each other, and to patterns exhibited by other Mexican taxa with northern affinities. These included two other platynine genera occurring in Mexico; Elliptoleus and Calathus (Liebherr, 1991c). Also analyzed was a clade of three Notiobia species-brevicollis, cyanippa and hilariola-restricted to northern Mexico, with species in the sister group found either in eastern North America or Mexico (Noonan, 1973). A sixth group comprising the two Mexican species of Lor-icera-rotundicollis and aptena-was also investigated (Ball and Erwin, 1969). All six groups acribe to Halffter's $(1976,1987)$ Nearctic pattern, whereby Mexican groups have sister groups in North America north of Mexico.

Species of Elliptoleus and Calathus are restricted to habitats in the pine-oak forest zone, making lowland corridors such as the Isthmus of Tehuantepec or the Rio Balsas

## B A A' A"C D <br> 



Figs. 53-58. Fundamental area cladograms for six groups of Carabidae derived using Assumption 0.53. Cladogram based on Elliptoleus species (Liebherr, 1991c). 54. Cladogram based on Calathus species (Liebherr, 1991c). 55. Cladogram based on Agonum cyclifer species group. 56. Cladogram based on clade of Agonum extensicolle species group. 57. Cladogram based on clade of Notiobia, subgenus Anisotarsus. 58. Cladogram based on two species of Loricera.
formidable barriers. The species of the cyclifer group are similarly restricted to habitats above 750 m elevation, though these species occur in open situations such as pastures as well as forest habitats. Likewise, two of the three species of the extensicolle group clade-A. cyanope and A. extimum - are recorded from above 900 m elevation. The third species, $A$. parextimum, has been collected from localities along the coast of Sonora and Sinaloa.

The three species of Notiobia are restricted to forests, either pine-oak forests from 500 to about $3,000 \mathrm{~m}$ elevation for $N$. brevicollis, or thorn forest, pine-oak forest, or cloud forest from 1,400 to $2,600 \mathrm{~m}$ elevation for $N$. cyanippa and N. hilariola (Noo-


Figs. 59, 60. Consensus area cladograms. 59. Nelson consensus of components observed in fundamental area cladograms (Figs. 53-58). Area $\mathbf{S}$ is connected by dashed line as it is represented in only one fundamental area cladogram (Fig. 56). 60. Nelson consensus cladogram modified to more heavily weight area relationships supported by representative endemic species at the expense of area relationships dictated by widespread species.
nan, 1973). Likewise, the Loricera species live in pine-oak or coniferous forest, with L. rotundicollis found above $1,700 \mathrm{~m}$ elevation, and L. aptena restricted to sites above $2,200 \mathrm{~m}$ elevation (Ball and Erwin, 1969). Interestingly, L. aptena is found only in the small area of endemism near La Ciudad, Durango that is also defined by the distribution of Elliptoleus olisthopoides (Liebherr, 1991b, c; Fig. 48, area B).

For this analysis, the extremely small areas of endemism defined by species distributions in Elliptoleus (Liebherr, 1991b) were combined so that contiguous regions of upland habitat were considered single areas of endemism (Fig. 48). Area A, considered the Sierra Madre Occidental and its eastern slope in Liebherr (1991c), was expanded to include adjacent lowland areas associated with the Rio Grande. A Sonoran desert area of endemism (Fig. 48, area S) was added to accommodate the range of Agonum parextimum. The Chiapan-Guatemalan highlands (Fig. 48, area $\varnothing$ ) were added to accommodate the ranges of Agonum patinale and Loricera rotundicollis. Amalgamation of areas of endemism switched the focus of the analysis to a search for broad-scaled general patterns of area relationships shared by these four different groups. The analysis followed the procedures detailed in Liebherr (1991c), which are not repeated here. Component analysis utilized the COMPONENT program (Page, 1989).

Fundamental area cladograms for Elliptoleus (Fig. 53) and Calathus (Fig. 54) were derived by translating the areas of endemism in Liebherr (1991c) to those used herein. For the cyclifer species group, the taxon-area cladogram (Fig. 49) analyzed under Assumption 0 resulted in a single fundamental area cladogram (Fig. 55). The taxonarea cladogram for the extensicolle group clade (Fig. 50) when analyzed under Assumption 0 resulted in 3 equally parsimonious fundamental area cladograms. These were summarized as a strict consensus tree (Fig. 56). The taxon-area cladogram for the Notiobia clade resulted in 105 equally parsimonious cladograms when analyzed under Assumption 0, which when summarized by strict or Nelson consensus, resulted in a fundamental area cladogram that only resolved areas C and D as sisters (Fig. 57). The two taxon cladogram for Loricera (Fig. 52) defined 3 equally parsimonious area cladograms under Assumption 0, which when summarized using strict consensus placed area B as the sister area to the unresolved areas C , D and $\varnothing$ (Fig. 58).

These six fundamental area cladograms (Figs. 53-58) share cladistic information that can be summarized by Nelson consensus (Fig. 59). The Chiapan-Guatemalan highlands are represented by the a portion of the distribution of $A$. patinale of the cyclifer group (Figs. 27, 49), and a portion of the distribution of L. rotundicollis (Fig. 52). In the general area cladogram, this area is placed in an unresolved position at the base of the cladogram reflecting the very different relationships shown by this area based on the two taxa residing there.

In the analysis of Calathus and Elliptoleus alone (Liebherr, 1991c), a basal sistergroup area relationship between the Sierra Madre Occidental and associated areas $\left(A+A^{\prime}+A^{\prime \prime}+B\right)$, versus the Transvolcanic Sierra plus Sierra Madre del Sur (C + D) was indicated. Based on consensus of these six groups, area B exhibits ambiguous relationships to either the Transvolcanic Sierra (areas C + D) or the Sierra Madre Occidental and associated deserts (areas $S, A, A^{\prime}$, and $A^{\prime \prime}$ ). This ambiguity is due to the use of Assumption 0, with its preferential representation of area relationships based on distributions of widespread species. In this case, the widespread distributions of $A$. anthracinum, A. scutifer (Fig. 49), A. cyanope (Fig. 50), and N. brevicollis (Fig. 51) outweighs the information based on representative species in areas A, B, C, and D in Elliptoleus (Fig. 53; Liebherr, 1991c: fig. 6). Likewise, the species of Calathus found only in the Sierra Madre Occidental areas A and B (Liebherr, 1991c: fig. 7) are discounted. Because the ambiguity of area B's relationships is introduced by methodological constraints that run counter to phylogenetic information of representative endemics in the various areas, I propose to modify the general area cladogram, allying area B with the more northerly areas (Fig. 60).

The data for Loricera supports the distinction of area B from C and D, based on endemism of $L$. aptena in the former, and the more southerly distribution of $L$. rotundicollis. The modified area cladogram (Fig. 60) predicts that if a Loricera species is found further north in the Sierra Madre Occidental, it will be either L. aptena, or the sister taxon to this species.

Ball (1970) noted that among the genera Carabus, Notiophilus, Loricera, Trechus and Calathus, only one species of Carabus is found in the mountains north and south of the lowlands of southeastern Arizona (areas A and $\mathrm{A}^{\prime \prime}$ ), suggesting a great age to this barrier. However, these areas are considered recently related based on this analysis (Figs. 59, 60). This disparity is no doubt based on Ball's consideration of taxa in boreally distributed Holarctic genera, illustrating a different set of area relationships than exhibited in taxa discussed herein. During periods in which the southeastern Arizona lowlands have been anathema for boreally adapted taxa, less boreally adapted groups such as the cyclifer and extensicolle species groups of Agonum would have had opportunities to exist in it, and thereby not respond to it. Moreover, in the case of Calathus, even though no species occurs on either side of this barrier (Liebherr, 1991c: fig. 7), area $A^{\prime \prime}$ is still shown to be most closely related to the Sierra Madrean areas A and B (Fig. 54) based on the phylogenetic relationships of the species occupying those areas.

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# ON THE SPIDER GENUS MELEON WANLESS (ARANEAE: SALTICIDAE) 

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#### Abstract

The genus Meleon Wanless is restricted to three African species: M. guineensis (Berland and Millot), M. solitaria (de Lessert) and M. kenti (de Lessert). Linus guineensis Berland and Millot is removed from the synonymy of $M$. solitaria and re-established as a valid species. Portia falcifera Wanless is placed in the synonymy of M. solitaria, while a male previously assigned to $M$. solitaria is considered the male of M. guineensis. Portia oreophila Wanless is placed in the synonymy of Portia madagascarensis Wanless. Meleon madagascarensis and M. russata (Simon) are shown to be misplaced in Meleon.


The genus Meleon, with Portia kenti de Lessert as type species, was established by Wanless (1984) for six species of jumping spiders which had previously been placed in Portia (Wanless, 1978; Murphy and Murphy, 1983). These species are (after Wanless, 1984:195):
M. falcifera (Wanless)-ô Uganda
M. kenti (de Lessert)- ${ }^{\circ} 9$
M. madagascarensis (Wanless)-ô Madagascar
M. oreophila (Wanless)-¢ Madagascar
M. russata (Simon)-\% Madagascar
M. solitaria (de Lessert) - ${ }^{\circ} \neq$ Guinea, Ivory Coast, Zaire

According to Wanless (1984:143) "[the] hyaline socket of the palpal tibial apophyses (sic) is synapomorphic for Meleon." Refering to the same feature Wanless (1984: 187) stated that "the male palps [of Meleon species are] easily recognised by the membranous socket of the tibial apophyses." A re-examination of Meleon and related taxa (Salticidae: Spartaeinae) reveals that although a membranous or hyaline tibial apophyseal socket is present in the known males of Wanless's Meleon species, a similar feature is shown also by species of several other spartaeine genera, notably Cyrba, Gelotia and Cocalus. It would thus appear that this character, as formulated by Wanless, cannot serve as a synapomorphy for Meleon. However, evidence from other characters indicates that Meleon kenti and some, but not all, of the other species included by Wanless in Meleon do form a monophyletic (natural) group. These characters include the following: (1) base of retrolateral tibial apophysis (proximal to socket) dorsally directed in the form of an inverted ' $L$ ', (2) cymbium proximally with a vertical retrolateral membranous fissure and (3) epigynal integument membranous anteriorly around copulatory orifices. In addition, the shape of the carapace in profile is fairly distinctive in $M$. kenti and close relatives, being elevated, with the highest point at or about the level of the second eye row (not at the level of the third eye row, as in Portia and several other spartaeine genera), with the anterior cephalic declivity much steeper than the posterior thoracic declivity. However, a similar
carapace form is shown by some other taxa, notably Veissella durbanii (Peckham and Peckham) within the Spartaeinae and, outside the Spartaeinae, by Lyssomanes, and thus should be viewed with some caution. Similarly, the shape of the cymbium (dorsal or ventral) in Meleon kenti and close relatives is fairly distinctive but the significance of this, too, is uncertain.

Reexamination of the material studied by Wanless necessitates some nomenclatural changes and reassociation of sexes. In his earlier revision of Portia (=Linus), in which Meleon species were previously included, Wanless (1978) synonymized Linus guineensis Berland and Millot, 1941 (female holotype from Kankan, Guinea) with Portia solitaria de Lessert, 1927 (female holotype from Medje, Zaire). As shown below, however, M. guineensis proves to be a valid species quite distinct from M. solitaria. In the same work Wanless described a male from Uganda as a new species, Portia falcifera. Subsequently, Wanless (1984) assigned a male Meleon from the Ivory Coast to the species $M$. solitaria. With the recognition of M. guineensis as a valid species, and taking into account the locality data of Meleon specimens in collections, it seems likely that the 'solitaria' male of Wanless is in fact conspecific with M. guineensis, while falcifera appears to be the true male of M. solitaria. The synonymy by Wanless [in Murphy and Murphy (1983)] of Portia cazomboensis Wanless, 1978 (female holotype from Cazombo, Angola) under Portia kenti de Lessert, 1925 (male holotype from Umbilo, Natal, South Africa) is accepted here. Thus the genus Meleon, as restricted above, appears to contain only three species, all known from both sexes: M. guineensis (Berland and Millot, 1941), M. kenti (de Lessert, 1925) and M. solitaria (de Lessert, 1927).

In addition to the species discussed above, Wanless (1984) transferred to Meleon three other spartaeine species which had previously been included in Portia: M. madagascarensis (Wanless, 1978) (male holotype from Mt. Ambohisanga, Madagascar), M. oreophila (Wanless, 1978) (female holotype from Mt. Ambohisanga, Madagascar) and M. russata (Simon, 1900) (female holotype from Antongil, Madagascar). The identical locality data and similar structure of madagascarensis and oreophila (e.g., carapace profile, cheliceral dentition, clypeal setae, leg spination) strongly suggest their conspecificity. Wanless's decision to maintain them as separate species was evidently due to the fact that oreophila (female) has a faint striped dorsal pattern and very short but distinct ventral hair fringes on the anterior legs whereas madagascarensis (male) is uniformly colored and lacks ventral leg hair fringes. Sexual dimorphism is widespread and common among salticids (see Peckham and Peckham, 1889) but usually involves conspicuous color patterns and structural features in males, females as a rule being less strikingly modified. However, in spite of the more distinctive female color pattern, the available evidence favors regarding madagascarensis and oreophila as the male and female of a single species. This evidence is as follows: (1) leg hair fringes: these are usually better developed in females than in males among those spartaeine salticids that possess them, thus the difference between madagascarensis and oreophila may not be significant; (2) cheliceral dentition: very similar in both species, consisting of three promarginal teeth with the middle tooth largest and six retromarginal teeth with the first distal smallest and slightly set apart from the rest (absent in right male chelicera); (3) leg spination: the number and position of leg spines in the two species is very similar, with identical retrolateral and dorsodistal femoral series; (4) carapace form: similar in the two taxa, being


Figs. 1-8. Meleon guineensis (Berland and Millot) and Meleon solitaria (de Lessert), female genitalia and carapace. 1-3, 7. M. guineensis. 4-6, 8. M. solitaria. 1, 4. epigynum (ventral view). 2, 5. spermathecae and ducts (dorsal view). 3, 6. spermathecae and ducts (dorsolateral view). 7, 8. carapace (lateral view).
moderately high and wide with the dorsum rounded in profile; (5) clypeal setae: the two pairs of clypeal setae below the anterior median eyes are anteriorly directed and long in both species; (6) carapace guanine deposits: both species show extensive whitish subintegumental guanine deposits in the ocular area of the carapace. On the
basis of these features Portia oreophila Wanless is here considered a synonym of Portia madagascarensis Wanless (NEW SYNONYMY). 'Meleon' madagascarensis does not show any of the synapomorphies of Meleon as specified above but instead has a stout, dorsally curved embolus and anteriorly-shifted embolar base as in the south Asian genera Cocalus and Gelotia, a special tibio-cymbial articulation as seen also in some species of Gelotia, and a distinctive epigynum. Similarly, 'Meleon' russata (Simon), known only from the female, shows no features (e.g., carapace shape) justifying its placement in Meleon; its spermathecae are small, hemispherical, with very short copulatory ducts. No derived features are known which associate russata with any other genus and until the male is discovered its systematic position is likely to remain enigmatic.

The format of description follows Wanless (1984). Synonyms listed by Wanless (1978) are not repeated here. Abbreviations of collections are as follows: AMNH— American Museum of Natural History, New York; BMNH - The Natural History Museum, London; MCZC-Museum of Comparative Zoology, Cambridge, Massachusetts; MHNG-Muséum d’Histoire Naturelle, Geneva; MNHN-Muséum National d'Histoire Naturelle, Paris; MRAC-Musée Royal d'Afrique Centrale, Tervuren; NMSA-Natal Museum, Pietermaritzburg.

## Meleon guineensis (Berland and Millot) STATUS REVISED

(Figs. 1-3, 7)
Linus guineensis Berland and Millot, 1941:399, figs. 92D, G, H (female holotype from Kankan, Guinea, MNHN, examined); Wanless, 1978:91, fig. 3F (as synonym of Portia solitaria).
Meleon solitaria: Wanless, 1984:187 (male, misidentification).
Diagnosis. Females of $M$. guineensis resemble those of $M$. solitaria in having a U-shaped anterior epigynal invagination but can be distinguished by the dorsally flexed ducts and the dorsal membranous folds around the copulatory openings. Males may easily by distinguished from other species by the elongate, curved embolus and the distinctive spiny dorsal cymbial apophysis.
Male. Described as Meleon solitaria by Wanless (1984:187).
Female (holotype, in fair condition). Carapace: pale reddish orange; sparsely clothed with recumbent translucent or white hairs with some darker hairs above margins and on thoracic region. Eyes: encircled with black; fringed with pale hairs, tuft-like behind PME. Clypeus: pale reddish orange, margin narrowly blackish; with medial setal triad, single seta below each AME, row of long setae at margin; Chelicerae: pale reddish orange; paturon anteriorly with many long setae and scattered pale hairs; promargin with three teeth, retromargin with four. Maxillae: pale reddish orange, with dark streak basally. Labium: reddish orange. Sternum: buffy yellow with darker margins, clothed with fine erect hairs. Coxae: similar to sternum, smooth. Abdomen: dorsally pale cream or whitish, anteriorly greyish at sides; two pairs of small sigilla; clothed with adpressed amber hairs (mostly rubbed off); ventrally whitish, with greyish median stripe from epigastric furrow to (and encircling) spinneret bases. Legs: buffy yellow with traces of darker annulations on femora, tibiae and metatarsi; ventrodistal hair fringes on tibiae II slight, marked on tibiae IV; spines numerous, strong. Legs I (both) missing. Palp: slender, whitish, tarsus apically buffy, femur with basal blackish prolateral spot; strong spines only on femur; tibia and tarsus clothed with
numerous long white hairs. Epigynum: anterior invagination recurved with numerous dorsal membranous folds; spermathecae elongate-pyriform; ducts strongly flexed dorsally.

Dimensions (mm): total length 6.85 ; carapace length 2.88 , breadth 2.30 , height 1.83; abdomen length 3.70 ; eyes, anterior row 1.56 , middle row 1.22 , posterior row 1.46; quadrangle length 1.25 ; diameters, AME 0.54, ALE 0.30, PME 0.23, PLE 0.26 ; interocular distances AL-PM-PL 0.30-0.45; clypeus 0.23.

| Legs | 1 | 2 | 3 | 4 | Palp |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Femur | - | 2.50 | 2.20 | 2.65 | 1.14 |
| Patella | - | 1.13 | 0.98 | 1.03 | 0.59 |
| Tibia | - | 1.86 | 1.58 | 2.21 | 0.75 |
| Metatarsus | - | 1.90 | 2.00 | 3.15 | - |
| Tarsus | - | 0.87 | 0.80 | 0.81 | 1.23 |
| Total | - | 8.26 | 7.56 | 9.85 | 3.71 |

Distribution. Tropical West Africa.
Material examined. Guinea. Kankan: 19 (MNHN) (holotype of Linus guineensis, determined as Portia solitaria by Wanless, September 1974); Ivory Coast. Kotiessou (environs of): 1 ô (J. Jezequel, MNHN: PNB.145) (determined as Meleon solitaria by Wanless, 1982).

## Meleon solitaria (de Lessert)

(Figs. 4-6, 8)
Portia solitaria de Lessert, 1927:425, fig. 14 (inverted!) (holotype female from Medje, Zaire, AMNH, examined).
Portia falcifera Wanless, 1978:111, figs. 14B, E-F, 15B-D (holotype male from Mpanga forest, Uganda, BMNH, not examined). NEW SYNONYMY.

Diagnosis. Females of $M$. solitaria resemble those of M. guineensis in having an anterior epigynal invagination in the form of an inverted ' $U$ ' but can be distinguished by the spherical spermathecae and parallel ducts. Males can be distinguished by the stout, moderately long embolus and the apically elongate and strongly curved retrolateral tibial apophysis.

Male. Described as Portia falcifera by Wanless (1978).
Female. Described by Wanless (1978) (excluding references to guineensis).
Distribution. Central and East Africa.
Material examined. Zaire. Medje: 1 it (AMNH) (holotype of Portia solitaria de Lessert).

## Meleon kenti (de Lessert)

Portia kenti de Lessert, 1925:339, figs. 8A-D (holotype male from Umbilo, Natal, South Africa, NMSA, examined); Wanless, 1978:111, figs. 14A, C-D, 15A; Murphy \& Murphy, 1983:39.
Portia cazomboensis Wanless, 1978:90, figs. 2A-D (holotype female from Cazombo, Angola, BMNH, not examined); Murphy \& Murphy, 1983:39 (as synonym of Portia kenti).

Diagnosis. Males of $M$. kenti can be distinguished easily by the short embolus. The epigynum of females lacks the recurved anterior invagination seen in the other two species, having this area smooth with a pair of weak folds extending laterally from the copulatory openings; the spermathecae are pyriform, with the narrowed anterior ends (ducts) angled laterally.

Male. Described by Wanless (1978).
Female. Described (as Portia cazomboensis) by Wanless (1978).
Variation. The copulatory openings of the epigynum are spaced apart in South African (Natal) specimens but situated closer together in the female from Malawi.

Distribution. Southern Africa.
Material examined. Malawi. Chintheche, $11^{\circ} 50^{\prime} \mathrm{S}, 34^{\circ} 13^{\prime} \mathrm{E}: 1 \delta^{\circ}, 1$, , January-February 1976 (R. Jocqué, MRAC: 147.921); South Africa. Durban, Natal: 18 (MCZC, in vial of Veissella durbanii); Umbilo, Durban, Natal: $1 \hat{o}$ (Kent, NMSA; palp, MHNG) (holotype of Portia kenti de Lessert); Rosi Bay, Toppin: 1 (NMSA: 9925, ex 1957 part) (paratype of Portia cazomboensis Wanless).

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# SYNOPSIS OF THE SAICINAE (HETEROPTERA: REDUVIIDAE) OF AMERICA NORTH OF MEXICO, WITH THE DESCRIPTION OF A NEW SPECIES OF SAICA FROM THE EASTERN UNITED STATES 

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#### Abstract

A new species of Saica is described from eastern United States. The forewing, male genitalia, and apex of the male and female abdomen are illustrated. A key to the Saicinae in America north of Mexico is provided and notes are provided for the other members of the subfamily in this geographic area.


This is the second in a series of papers dealing with the Saicinae of the Western Hemisphere. The subfamily Saicinae is distributed throughout the world with 21 genera and 140 species listed by Maldonado-Capriles (1990). The subfamily attains its greatest species diversity in Southeast Asia and Africa where about 47 species and 35 species, respectively, have been described. In North America the subfamily is small, being represented by only three genera and five species, including the one described below.

In this paper a new species of Saica is described from eastern North America and a key is provided to separate the saicine species recorded from America north of Mexico. Information on distribution and habits of the other species in the subfamily is provided. Label data for the holotype is quoted exactly using a slash (/) to indicate separate lines of a label and a semicolon to indicate separate labels. Measurements are in millimeters; measurements in parentheses are of the holotype.

The following abbreviations are for institutions and their curators who kindly lent material used in this study: CBB-Cheryl B. Barr (private collection), Louisiana State University, Baton Rouge; LSU-Louisiana State University, Baton Rouge, J. B. Chapin; MSS—Mississippi Entomological Museum, Mississippi State, T. L. Schiefer; NCDA - North Carolina Department of Agriculture, Raleigh, K. Ahlstrom; UMC Wilbur R. Enns Entomology Museum, University of Missouri, Columbia, R. W. Sites; USNM-United States National Museum of Natural History, Washington, D.C., T. J. Henry.

Saica elkinsi, new species
Figs. 1-5
Diagnosis. This species is recognized by its uniformly yellowish brown coloration; dense, erect silvery pilosity; and the structure of the male hypopygium.

Description male. Dorsal Aspect: length 7.75-8.30(7.92) ( $\mathrm{N}=6$ ), width of abdomen 1.36-1.73 (1.36). Uniformly yellowish brown, apex of femora tinged with red in some specimens. Vestiture: uniformly clothed with decumbent silvery setae, interspersed with moderately dense erect silvery pilosity. Head: length $0.82-0.91$ ( 0.82 ), width


1


2


Figs. 1-5. Saica elkinsi. 1. Right forewing. 2. Hypopygium, posterior view. 3. Paramere, lateral view. 4. Apex of male abdomen, dorsal view. 5. Apex of female abdomen, lateral view.
0.76-0.84 (0.78), vertex 0.45-0.47 (0.45). Rostrum: I, length 0.56-0.65 (0.60); II, 0.27-0.33 (0.29); III, 0.25-0.29 (0.27). Antenna: I, length 2.72-3.21 (3.02); II, 1.181.36 (1.27); III, 1.64-1.88 (1.73); IV, 1.05-1.33 (broken); segments I and II densely clothed with erect pilosity, length of pilosity equal to twice width of segment. Pronotum: impunctate; length anterior lobe $0.75-0.85(0.75)$, gibbosities well developed; length posterior lobe $0.68-0.75$ ( 0.68 ); humeral width $1.31-1.36$ (1.31), humeral spines $0.69-0.84$ ( 0.73 ), sparsely beset with pilosity on basal half; prosternal process $0.16-0.25$ ( 0.25 ), visible from above. Mesoscutum: spine, $0.91-1.16$ (apex broken), angled strongly caudid to curved sightly erect. Scutellum: basal process erect, apex entire, semicircular in caudal aspect; posterior spine, $0.14-0.23$ ( 0.14 ), sloping strongly caudad, lacking pilosity. Forewing: venation as in Figure 1, with two closed cells, membrane and veins yellowish, semi-transparent. Genitalia: pygophore (Fig. 2) with spines narrowly separated at base, curving strongly laterad, apices truncate with ventral angle strongly hooked. Parameres (Fig. 3) elongate-oval, apex rounded with small, poorly defined dorsal notch. Posterior margin of abdominal tergite VII rounded (Fig. 4).

Macropterous female. Similar to male in structure and coloration. Measurements: length $7.92-8.75(\mathrm{~N}=5)$, width of abdomen $1.70-1.92$. Head: length $0.85-0.96$, width $0.76-0.85$, vertex $0.45-0.49$. Rostrum: I, length $0.60-0.69$; II, $0.31-0.35$; III, 0.29-0.36. Antenna: I, length 2.79-3.25; II, 1.18-1.36; III, 1.75-1.80; IV, 1.09-1.18. Pronotum: length anterior lobe $0.85-0.93$, length posterior lobe $0.68-0.75$, humeral width 1.35-1.40, humeral spines $0.73-0.98$, prosternal process $0.19-0.22$. Mesoscutum: spine $0.96-1.31$. Scutellum: posterior spine $0.25-0.31$. Genitalia: spine on caudolateral margin of abdominal segment VII not well developed (Fig. 5).

Micropterous female. Similar to male and macropterous female in structure and coloration except abdomen pyriform and wings reduced to pad-like structures which only reach to mesoscutal spine. Measurements: length $7.85(\mathrm{~N}=2)$, width of abdomen $2.30-2.42$. Head: length $0.95-1.00$, width $0.80-0.82$, vertex $0.49-0.55$. Rostrum: I, length $0.65-0.67$; II, 0.35 ; III, 0.25 . Antenna: I, length $2.75-2.79$; II, 1.15-1.16; III, 1.45 ; IV, 1.02. Pronotum: length anterior lobe 0.95 , length posterior lobe $0.53-0.55$, humeral width $1.00-1.05$, humeral spines $0.71-0.76$, prosternal process $0.21-0.23$. Mesoscutum: spine 0.82-1.02. Scutellum: posterior spine 0.25-0.26.

Holotype. Male, labeled: "HOLOTYPE; RADFORD/ARSENAL, AT/LIGHT, 8-10-51/HOFFMAN; Saica/thrinaca/H\&E/1960/DET.J.C.ELKINS [manuscript name]; HOLOTYPE/Saica/elkinsi/Blinn 1992." Deposited in the USNM.

Paratypes. ARKANSAS: 19, Polk Co., S. of Board Camp, R29W T35SE Sec. 22, 17-20-VIII-1985 (CBB); FLORIDA: 19, Marion Co., Dunnellon, 12-VI-1939 (USNM); 1ô, Pinellas Co., Dunedin, 22-IV-1925 (USNM); LOUISIANA: 1ô, East Baton Rouge Parish, Baton Rouge, 19-VI-1973, light trap (LSU); 1ô, Washington Parish, Lee Mem. For., Sheridan, 7-VIII-1985, MV \& BL (LSU); MISSISSIPPI: 1̂̂, Oktibbeha Co., Starkville, 11-VIII-1975, blacklight trap near edge of deciduous woods (MSS); 18, 30-VI-1975, blacklight trap near edge of deciduous woods (MSS); 1 [abdomen missing], 28-VI-1975, blacklight trap near edge of deciduous woods (MSS); MISSOURI: 2오, Boone Co., 1.3 mi . N Ashland Wildlife Area, 5-VI-1981, tall fescue D-Vac sample (UMC); 1ô, Callaway Co., Tucker Prairie, 8-VIII-1968 (UMC); NORTH CAROLINA: 1 , Carteret Co., Morehead City, 27-VII-1970 (NCDA); 1ô, Wake Co., SHE\&EC, New Hill, 13-VI-1979, at lights (NCSU); VIRGINIA: 1̂̂, 1 ㅇ, Chatham Co.,
W. Tarpley, 27-VII-1963, blacklight trap (USNM); 1̊̂, Montgomery Co., Blacksburg, 13-VIII-1974 (USNM); 1ல̂, 13-VII-1952, at light (USNM).
Remarks. Hoffman (1953) first recorded this species from Virginia as Saica fuscovittata Barber (=Pseudosaica florida (Barber)) and commented on its unusual occurrence in southwestern Virginia. Many of the specimens examined were collected at night, either at ultraviolet or mercury vapor lights. The two micropterous females collected in Missouri may give us our best clue as to the habits of this species. These specimens were collected in a mixed tall fescue field using a D-Vac sampler. It may be that $S$. elkinsi is a ground dwelling predator associated with grasses or other herbaceous plants. This idea is further supported by the additional Missouri specimen collected at Tucker Prairie, a native short-grass prairie. This is similar to what is known about the habits of Oncerotrachelus acuminatus (Say) and Pseudosaica florida (Barber) (see below).

Etymology. This species is named in honor of J. C. Elkins who was the first to recognize it as undescribed and who has contributed to our knowledge of the Saicinae.

KEY TO THE SAICINAE IN AMERICA NORTH OF MEXICO

1. Pronotum armed with spines near humeral angles, scutellum with spine erect ......... 2

- Pronotum unarmed, scutellum with spine strongly reclined ............................. 4

2. Process of male hypopygium a single erect spine, posterior margin of abdominal ster-
num VII in females sloping ventrocephalad, antennal segment II subequal to one-third
length of antennal segment I ............................ . . . seudosaica florida (Barber)

- Process of male hypopygium bifurcate (Fig. 2), posterior margin of abdominal sternum VII in females vertical to subvertical (Fig. 5), antennal segment II subequal to onehalf length of antennal segment I 3

- Forewing with three closed cells, general coloration red, brachyptery unknown in females...................................... . . Saica apicalis Osborn \& Drake

4. Dorsum with a broad fuscous stripe extending along midline, antennae and legs densely pilose

Oncerotrachelus acuminatus (Say)

- Dorsum uniformly pale yellow, antennae and legs without dense pilosity

Oncerotrachelus pallidus Barber

## NOTES ON OTHER SAICINAE IN AMERICA NORTH OF MEXICO

Oncerotrachelus acuminatus (Say). This species is widely distributed in the eastern United States, having been recorded from New England south to Florida and west to Texas and Minnesota (Froeschner, 1988). McPherson (1992) recently recorded this species from Michigan. Little is known regarding the habits of this species. Blatchley (1926) reported finding up to 50 individuals hibernating beneath logs in Indiana. It is often collected at night using ultra violet lights. Additional specimens have been collected sweeping grasses, using a D-Vac sampler in tall fescue fields, and sweeping native prairies in Missouri.

Oncerotrachelus pallidus Barber. O. pallidus is known only from Texas and Oklahoma (Froeschner, 1988). Nothing is known regarding the biology of this species.

Pseudosaica florida (Barber). Originally described in the genus Saica, P. florida was transfered to the genus Pseudosaica by Blinn (1990) based on characteristics of
the male hypopygium. It is known only from Florida and Mississippi, where it has been collected from Spartina cynosuroides and Juncus roemerianus using Berlese funnels.

Saica apicalis Osborn and Drake. Elkins (1951) recorded this species from Texas based on a single specimen collected at light in Texarkana. This species is widely distributed in Central America south of Mexico. Its presence in the U.S. may be a result of an accidental introduction of an exotic species or a labelling error. It is easily distinguished from $S$. elkinsi by the presence of three closed cells in the forewings.

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# OLIGEMBIA VETUSTA, A NEW FOSSIL TERATEMBIID (EMBIOPTERA) FROM DOMINICAN AMBER 

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Abstract.-A new species, Oligembia vetusta, is described on the basis of a male in lower Tertiary amber from the Dominican Republic. The new species is the first fossil representative of the family Teratembiidae. The systematic position of the new species is discussed, as is the paraphyletic nature of the genus Oligembia. A cladogram of teratembiid genera is presented.

There are few records of fossil Embioptera. Until now, only two species from amber have been described: Electroembia antiqua (Pictet, 1854) from Baltic amber and Burmitembia venosa Cockerell, 1919 from Burmese amber.

David Grimaldi, of the American Museum of Natural History, has kindly provided for study two male Embioptera in Dominican amber. The amber is from the Lower Tertiary (ca. 25-30 my). A review of the evidence for this dating is provided by Grimaldi (1991).

In one of those two specimens, the abdominal terminalia (which provide most of the characters used at lower taxonomic levels) are unfortunately not preserved. The size, type of mandibles, wing venation, and shape and chaetotaxy of the hind basitarsus, suggest that this specimen belongs in the family Anisembiidae.

The other specimen is well preserved and belongs to the family Teratembiidae. This family is composed of three American genera (Diradius Friederichs, 1934 and Oligembia Davis, 1939 with species from Texas to Argentina including Caribbean islands, and Teratembia Krauss, 1911 with species from Argentina, Paraguay, and Brasil) and one African genus (Paroligembia Ross, 1952, with a single species from Angola). The new species has a character combination that clearly excludes it from Teratembia, Diradius, or Paroligembia, and would place it in the genus Oligembia. However, all the characters previously proposed as diagnostic for that genus (Ross, 1984) are actually found in only some of its species or are synapomorphies for Teratembiidae in general (Szumik, 1991).

An analysis of the higher classification of the order is presently being completed (Szumik, ms.). In that study, 36 characters are used in a cladistic analysis of 41 species (representing 32 genera from 8 families); Teratembia (the only genus of Teratembiidae analyzed there) appeared within the family Oligotomidae (Fig. 1).

Oligotomidae has three genera: Oligotoma Westwood, 1837 from the Indian region, Aposthonia Krauss, 1911 from Australia and tropical Asia, Indonesia, and Melanesia (Ross 1963:135), and Haploembia Verhoeff, 1904 from the Mediterranean and Black Sea.

In the analysis of Szumik (ms.; relevant results summarized in Fig. 1) the group Teratembia + Oligotomidae was supported by the posterior half of the right tenth hemitergite separated from the rest of the tergite.

Table 1. Data matrix.

|  | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Outgroup | 0 | 0 | 0 | 1 | 0 | - | 0 | 0 | 0 | - | - | - | 0 |
| A. glauerti | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | - | - | 1 | 0 |
| A. gurneyi | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | - | - | 1 | 0 |
| H. solieri | 0 | 0 | - | 1 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 0 |
| O. nigra | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 |
| O. saundersii | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 |
| D. erba | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 4 | 0 | 1 |
| D. plaumanni | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 4 | 0 | 1 |
| O. hubbardi | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 4 | 0 | 1 |
| O. melanura | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 1 |
| O. mini | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 3 | 0 | 1 |
| O. peruviana | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| P. angolica | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| T. geniculata | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 4 | 0 | 1 |
| O. vetusta | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 1 |

Teratembia + Oligotoma + Aposthonia share the absence of a middle bladder on the hind basitarsus (char. 0), the hind basitarsus narrow and with few hairs (char. 1 ), and the process of the right hemitergite of tenth abdominal tergite with a small thorn on the dorsal face (char. 6). The presence of a basal process on the left cercus appeared as an autapomorphy of Teratembia (as seen below, this is actually a synapomorphy of Teratembiidae, and its presence in some Oligotoma is a parallelism).

In that larger study (Szumik, ms.) the only representative of the Teratembiidae used is the genus Teratembia. That analysis, therefore, does not provide any information on the monophyly of the Teratembiidae or their interrelationships. A more detailed analysis (including all the described genera of Teratembiidae) is made here, to give some insight on the relationships between the teratembiid genera and to place the new species.

## METHODS

Fourteen species were used in this analysis (see data matrix in Table 1). Five of them (Fig. 1) had been used in the larger analysis (Szumik, ms.), to which Oligembia vetusta and eight other described species of Oligotomidae and Teratembiidae were added. Paroligembia angolica Ross, 1952 was the only species for which I did not see specimens; this species was scored on basis of the original description. The outgroup has the character states of the common ancestor of Oligotomidae +Ter atembia in the most parsimonious tree found in Szumik (ms.).

A method for weighting characters according to their homoplasy is used here. The method is based on searching "heaviest trees," with character weights defined as a concave function of homoplasy (Goloboff, 1993a).

Hennig86 (Farris, 1988) was used to find the shortest tree(s) for the equally weighted data, Pee-Wee (Goloboff, 1993b) used to weight the characters and to find the heaviest tree(s), and Clados (Nixon, 1992) used to produce tree diagrams.


1


Figs. 1, 2. 1. Relationship of Oligotomidae and Teratembiidae proposed in Szumik (ms.). 2. Strict consensus of two trees produced by data matrix in Table 1.

Parallelisms observed in taxa outside the ingroup were considered when calculating the weight of the characters analyzed here (Pee-Wee calculates character weights as $30 /(3+\mathrm{R}+\mathrm{ES})$, where R is the variation outside the ingroup and ES is the extra steps on the tree).

In this analysis the ambiguous optimizations were not considered as support for any clade. The consensus tree (Fig. 2) does not show one optimization, but instead those synapomorphies common to all possible dichotomous parsimonious resolutions (Goloboff, 1993b).

Abbreviations for male terminalia follow Szumik (1991). Measurements are given in millimeters. Ocular ratio is defined in Szumik (1991).

## CHARACTERS

Eight of the 36 characters from the larger analysis were used (the other 28 characters were not used here, because they are not informative at the present taxonomic level). Five characters were added.
0) Middle bladder of the hind basitarsus (Davis, 1938): 0, present; 1, absent.

1) Form and chaetotaxy of the hind basitarsus: 0 , broad with many hairs on ventral area; 1 , narrow with few hairs on ventral area.
2) Wings, Ma vein (Davis, 1938): 0, forked; 1, unforked.


Figs. 3-6. Oligembia vetusta. 3. Submentum. 4. Right hind basitarsus, anterior view. 5. Terminalia, dorsal view. 6. Process of the left cercus, ventral view.
3) Apical process of the LC1: 0 , absent; 1 , present.
4) Basal process of the LC1: 0, absent; 1, present.
5) Process of the 10L: 0, leaf-like with a longitudinal ridge; 1 , subdivided in subequal inner and outer margins; 2, same as state 1 but inner and outer margins differentiated in hook and leaf-like portions.
6) Process of the 10R: 0, sharp hook; 1, leaf-like with a small thorn on the dorsal surface.

Table 2. Characters: extra steps, variation observed outside the group, fit.

| Char. | Ex. steps | O.v. | Fit |
| :---: | :---: | :---: | :---: |
| 0 | - | 6 | 3.3 |
| 1 | - | 5 | 3.7 |
| 2 | - | 1 | 7.5 |
| 3 | 4 | 1 | 3.7 |
| 4 | 2 | 1 | 5.0 |
| 5 | 2 | 8 | 2.3 |
| 6 | - | 5 | 3.7 |
| 7 | - | - | 10.0 |
| 8 | 1 | - | 7.5 |
| 9 | - | - | 10.0 |
| 10 | - | - | 10.0 |
| 11 | - | - | 10.0 |
| 12 | - | - | 10.0 |

7) Lpp: 0, normal; 1, hook-like.
8) Separation between MS and 10R: 0, without lines of fusion; 1, with lines of fusion; 2 , separated by a membranous area.
9) LCBP: 0, simple; 1 , complex.
10) Apex of the LCBP: 0, blunt; 1 , one spine (not sclerotized and not articulated with base); 2, one spine (sclerotized and articulated with base); 3, two spines (same as state 1 ); 4 , two spines (same as state 2).
11) $\mathrm{Hp}: 0$, plate-like form; 1 , tubular form.
12) Relation between MS and 10L: 0 , without lines of fusion; 1 , with lines of fusion.

## RESULTS AND DISCUSSION

Pee-Wee found 2 trees (the strict consensus of which is shown in Fig. 2) with total fit $86.7,29$ steps long. These trees are 1 step longer than the 236 trees found by Hennig86. The strict consensus of those 236 trees and those found by Pee-Wee would have in common the groups: Oligotomidae (without Haploembia) + Teratembiidae, Oligotomidae (without Haploembia), Teratembiidae, and Diradius erba Szumik, 1991 + D. plaumanni (Ross, 1944) (Fig. 2).

The monophyly of Teratembiidae is supported by the 10LP with inner and outer margins subequal (char. 5) and fusion lines between 10L and MS (char. 12). The group formed by $O$. vetusta and the rest of the teratembiids (Fig. 2) is supported by the apex of the LCBP with 2 points (char. 10). Although this character is the only one which supports that group, it does not have any homoplasy (Table 2).

It seems clear from this analysis that Oligembia is not a monophyletic group, and that the species included in the genus share no more than symplesiomorphies. If a new genus was created for the new fossil species, a new genus would be necessary for each species in the pectinate part of the cladogram (Fig. 2). For the moment, and given the preliminary nature of this analysis, $O$. vetusta is provisionally incorporated into the genus Oligembia, considering this as a parayphyletic group. I propose that those oligembids having a membranous area or lines of fusion between 10R and MS, and apex with two points (with an articulate base), and the genera Teratembia, Diradius, and Paroligembia, form a monophyletic group, and that their sister group is $O$. vetusta.

## Oligembia vetusta, new species

Figs. 3-7
Diagnosis. O. vetusta can be distinguished from other Oligembia by the following combination of characters: LCBP finishing in two short points no more sclerotized than the rest of the process, LCl curved, submentum strongly depressed around the margins, and no lines of fusion between 10RP and MS.

Type. Holotype male from Dominican amber in The American Museum of Natural History, New York.

Etymology. The specific name is a Spanish adjective for something old and obsolete.
Male holotype. As in Figure 7. Total length: 5.15. Head: rectangular, width/length, 0.72 . Ocular ratio: 0.66. Mandibles: teratembiid type. Submentum as in Figure 3. Wing lengths: anterior, 3.43 ; posterior, 2.80. Wing venation: R 1 and Cu conspicuous,


Fig. 7. Oligembia vetusta, holotype male (photograph by D. A. Grimaldi).

Rs + Ma and Rs more or less conspicuous, the rest marked by rows of macrotrichia. Cross veins: 2 to 3 between C and R1, 2 to 3 between R1 and Rs. Rs + Ma and Mp originating on a cross vein between R1 and Cu . Hind basitarus, length: 0.15 , width/ length: 0.33; setae as in Fig. 4. Terminalia: as in Fig. 5. 10R fused to the MS, no lines of fusion between them. Some lines of fusion (but shallow) between 10L and MS. 10R strongly depressed on the posterior margin. LCBP with two sharp, short points in the apex (Fig. 6), no more sclerotized than the rest of the process. Ventral terminalia not observable ( $\mathrm{H}, \mathrm{Hp}$ and LPPT obscured by a bubble).

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# A NEW SPECIES OF APHELOCHEIRUS FROM SUMATRA, AND ADDENDA TO THE WORLD CHECKLIST (HETEROPTERA: NAUCORIDAE) 

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#### Abstract

Aphelocheirus bengkulu n. sp. is described based on collections from southern Sumatra. Illustrations are provided of the dorsal habitus and the male and female genital structures. Supplemental couplets are given to incorporate this species into the key of Polhemus and Polhemus (1988) to species occurring in tropical Asia. Addenda are noted for the checklist of world Aphelocheirinae, based on recently published works.


A recent monograph on the Aphelocheirinae of tropical Asia (Polhemus and Polhemus, 1988) noted the presence of Aphelocheirus on Sumatra based on a single macropterous female from Medan, in the northwestern part of the island. Although the authors suspected at the time that this was an undescribed endemic Sumatran species, this female presented no distinguishing morphological characters that would allow it to be unambiguously separated from other Aphelocheirus species occurring in the Malay Archipelago, and in the absence of males it was decided to defer any description until more specimens became available.

Recent collections by the author and J. T. Polhemus in southern Sumatra during 1991 produced several series of Aphelocheirus containing both sexes. The species involved is indeed new, and described herein. The previously discussed female from Medan is morphologically similar to these series, and may be conspecific, but resolution of this matter awaits further material from northern Sumatra, since many genera of aquatic Heteroptera display allopatric speciation patterns between the northern and southern sections of the island.

In the following description CL numbers after localities refer to a system used to cross reference specimens and ecological data. Acronym designations for specimen repositories are given in the acknowledgments section.

## Aphelocheirus bengkulu new species

Figs. 1-5
Diagnosis. - Aphelocheirus bengkulu n . sp. may be distinguished from other known Aphelocheirus species in tropical Asia by the distinctive structure of the male parameres (Fig. 5). In the key of Polhemus and Polhemus (1988) to brachypterous forms this species runs to couplet 20 , where it may be separated by the absence of a gently raised longitudinal median carina on the abdominal venter, the presence of small peg-like setae medially on the posterior margins of abdominal tergites IV-VI, the structure of the male genitalia, and geographic provenance. The following new couplets may be inserted into that key to accomodate this new species.


3


Figs. 1-5. Aphelocheirus bengkulu n. sp. 1. Brachypterous male, dorsal habitus (legs omitted). Specimen from Hutabarna River, Sumatra. 2. Macropterous female, showing structure of embolar margin. Specimen from Pauh River, Sumatra. 3. Inner projection of left propleuron. Inner margin at top of figure. 4. Female subgenital plate, ventral view. 5. Male genital complex, dorsal view.

b. Abdominal sternites IV-VI (at least) with 3-6 small stout peg-like setae medially
on posterior margins; Australia or Sumatra ................................... 20a

20a. a. Abdominal venter with gently raised longitudinal median carina; male left paramere with rounded projecting tab on inner margin, tip acute; Australia

## A. australicus Usinger

b. Abdominal venter with a longitudinal glabrous stripe centrally, but lacking a gently raised longitudinal median carina; male left paramere lacking a rounded projecting tab on inner margin, tip expanded, broadly concave; southern Sumatra
A. bengkulu n . sp.

Description. - Brachypterous male: Of moderate size for genus, form ovate, length 6.72 mm ; maximum width (across abdomen) 4.51 mm (Fig. 1). Coloration dull medium brown, with head and genital capsule dark yellowish.

Head dark amber yellow, infuscated centrally, shining, alveolate, width/length = $1.56 / 1.06$, not exceptionally elongate, produced ahead of eyes for only 0.45 the length of an eye; eyes black, shining, width/length $=0.24 / 0.90$, lateral margins weakly sinuate, not exceeding adjacent anterolateral pronotal angles; anterior/posterior interocular $=1.15 / 0.74$.

Pronotum dark brown, yellowish laterally and medially, width/length (midline) $=$ $3.52 / 0.98$, surface coarsely rugose, shining centrally, bearing short recumbent gold setae, lateral margins narrowly glabrous and translucent, each with approximately 13 minute erect peg-like setae, posterolateral angles broadly rounded. Scutellum dark yellow, frequently infuscated basally, width/length $=1.88 / 0.82$, surface rugose, shining, bearing very short recumbent gold setae, lateral margins sinuate, basal margin broadly sulcate. Hemelytra dark brown, brachypterous, not attaining base of abdominal segment III, barely touching medially, surface rugose, with short fine recumbent gold setae, embolar margin coming to an acute angle, lacking peglike setae.

Abdomen dull dark brown, surface sparsely covered with recumbent gold setae, posterior margin of tergite V asymmetrically produced medially (Fig. 1), posterolateral angles of segments III-VII produced to short spines.

Ventral surface dull medium brown, weakly pruinose, sparsely covered with short recumbent gold setae; antennae pale yellow, lengths of segments $\mathrm{I}-\mathrm{IV}=0.08,0.12$, $0.28,0.44$; rostrum gold, glabrous, length 3.30 , attaining middle trochanters; prosternum reflexed anteromedially, longitudinally carinate medially, inner projection of propleuron broadly notched, apex acute (Fig. 3); mesosternal plate with sharp longitudinal medial carina, rising to a rounded tumescence posteromedially; abdomen with segments IV-VI with 4-6 short posteriorly directed peg-like setae medially along posterior margins, posterior projections of segment VII with apices acute, slightly exceeding tip of genital capsule.

Legs dark yellowish, clothed with fine recumbent gold setae; fore trochanter, femur, tibia and tarsi with thick hair pads on inner faces; fore, middle and hind coxae with combs of gold setae distally; middle trochanter, femur, tibia and tarsi with thick pads of gold setae posteriorly; middle femur with longitudinal row of short brownish spines ventrally, many short recumbent gold spines along anterior margin, 2 slender erect gold spines basally along posterior margin; middle tibia with scattered short stout brownish spines along anterior margin, 3 slender erect gold spines along posterior
margin, roughly longitudinal row of short brownish spinules ventrally parallel to posterior margin, transverse row of reddish spines apically; hind femur with very short sharp gold spines along anterior margin, scattered very short stout brown spinules ventrally; hind tibia with stout reddish spines along anterior margin, transverse row of reddish spines apically; hind tibia and tarsi with long swimming hairs on posterior faces; claws gently curving, gold, tips brown.

Male genitalia with right paramere expanded basally, narrowed and curving on distal half, with thick fringe of setae on outer margin; left paramere more massive, inner margin sinuate, outer margin bearing fringe of setae, distal portion expanded, tip concave (Fig. 5).

Brachypterous female: Similar to brachypterous male in general structure and coloration, length 7.13 mm ; maximum width 4.59 mm . Plates of abdominal segment VII with posterior margins weakly concave, subgenital plate broadly triangular, tip broadly rounded (Fig. 4).

Macropterous female: Similar to brachypterous form with following exceptions: length 7.45 mm ; maximum width 4.67 mm ; dorsal coloration uniformly dull dark brown, pronotum with lateral margins greatly expanded, posterolateral angles broadly rounded; scutellum swollen, mesoscutum evident, delineated by sinuate transverse furrow; hemelytra complete, wing membrane atrovelutinus, mostly disintegrated in single specimen at hand, hemelytral surface bearing recumbent gold setae, texture generally dull, with scattered glabrous areas on clavus and claval commissure, clavus and claval vein well defined, embolar margin gently curving laterally, coming to an acute angle posterolaterally (Fig. 2); prosternum not reflexed anteromedially; mesosternal plate broadly and gently tumescent.

Discussion.-On the basis of the male genitalia, Aphelocheirus bengkulu falls into a group of species characterized by the possession of a large, distally curving right paramere as viewed from above in the genital capsule (see Fig. 5) with a setose outer margin and a broadly expanded base. This group includes $A$. celebensis Polhemus and Polhemus, A. lorelindu Polhemus and Polhemus, and A. robustus Nieser and Chen, all species found on Celebes, plus A. pallens Horvath from New Guinea and A. australicus Usinger from northern Australia. The taxa in this group are distributed on the islands of the Malay Archipelago eastward to Australia, and are distinctive in their male genital architecture from the assemblage of species seen in Indochina, which have slender and acuminate right parameres. The right paramere of $A$. bengkulu is very similar structurally to that of $A$. lorelindu, whereas the left paramere is quite distinct, although perhaps closest to that of $A$. minor from Borneo. The female subgenital plate is relatively unmodified, and similar to that of australicus and pallens.

Etymology. - The name "bengkulu" refers to Bengkulu Province in southern Sumatra where the type series was collected.

Ecological notes. - The Hutabarna River at the type locality was a broad, unshaded stream flowing swiftly in a bed of scattered rocks and boulders intermixed with sand and coarse gravel. The Aphelocheirus were taken by disturbing the loose substrates in the channels between the boulders while holding a net downstream. Most captures were made in midstream sections, with few of the insects being taken near shore. The single specimen from the Ketelang River was taken from a patch of clean sand at the base of a vertical rock cliff swept by the current.

Material examined.-Holotype, brachypterous male: INDONESIA, Sumatra,

Bengkulu Prov., Hutabarna River at Tabarenah, 7 km . W. of Curup, 600 m ., water temp. $23.5^{\circ}$ C., 7 September 1991, CL 2582, D. A. and J. T. Polhemus (USNM). Paratypes: INDONESIA, Sumatra, Bengkulu Prov.: 7 brachypterous males, 5 brachypterous females, same data as holotype (JTPC, MZB, BPBM); 1 macropterous female, 3 brachypterous males, 2 brachypterous females, Pauh River, 25 km . SE of Muaraaman, 600 m ., water temp. $23^{\circ} \mathrm{C}$., 8 September 1991, CL 2584, J. T. and D. A. Polhemus (JTPC); 1 brachypterous male, Ketelang River, 39 km . SE of Muaraaman, 720 m ., water temp. $21.5^{\circ} \mathrm{C}$., CL 2585 , D. A. and J. T. Polhemus (JTPC).

## ADDITIONS TO THE WORLD CHECKLIST OF APHELOCHEIRINAE

Since the publication of the monograph by Polhemus and Polhemus (1988), two additional works dealing with tropical Asian Aphelocheirinae have appeared. The first was a set of supplemental corrections to the monograph's world checklist by J. T. Polhemus (1989), the second a work containing descriptions of new taxa from Borneo and Celebes (Nieser and Chen, 1991). It is anticipated that more new species will be discovered in the region, and further supplements to the monograph will be provided as these become necessary.

The following recently described taxa should be added to the world checklist presented by Polhemus and Polhemus (1988), and updated by J. Polhemus (1989):
bengkulu D. Polhemus, n. sp., 1991, J. New York Ent. Soc. Sumatra. breviculus Nieser and Chen, 1991, Tijd. voor Ent., 134:49. Borneo.
robustus Nieser and Chen, 1991, Tijd. voor Ent., 134:50. Celebes.

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The holotype of the new species described herein is deposited in the U.S. National Museum of Natural History, Washington, D.C. (USNM); paratypes are held in the Bishop Museum, Honolulu, Hawaii (BPBM), the J. T. Polhemus collection, Englewood, Colorado (JTPC), and the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB).

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Polhemus, D. A. and J. T. Polhemus. 1988. The Aphelocheirinae of tropical Asia (Heteroptera: Naucoridae). Raffles Bull. Zool. 36(2):167-300.
Polhemus, J. T. 1989. The Aphelocheirinae of tropical Asia (Heteroptera: Naucoridae)corrigenda and addenda. Raffles Bull. Zool. 37(1 \& 2):171-172.

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# plUSIOTIS CITLALTEPETLAMAYATLI, A NEW SPECIES OF THE LECONTEI GROUP FROM MEXICO (COLEOPTERA: MELOLONTHIDAE; RUTELINAE) 

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#### Abstract

A new species of the lecontei group of Plusiotis is described, based on recently collected material in the state of Veracruz, Mexico. The distinctive characteristics are illustrated, a key to separate the species of the lecontei group is presented, and its eco-geographical distribution is outlined and compared with that of the fir forest.


Resumen.-Se describe una nueva especie de Plusiotis del grupo lecontei con base en material recientemente colectado en el estado de Veracruz, México. Se ilustran sus caracteristicas distintivas comentando sus relaciones con las demas especies del grupo. Se presenta una clave para la separacion de las especies comprendidas dentro del grupo lecontei y por ultimo se comenta su distribucion ecogeográfica discutiendo sus relaciones con el bosque de abeto.

The lecontei species group comprises seven closely related species, which are distributed from the southwestern U.S. to the Guatemalan mountains at elevations between $2,000-3,800 \mathrm{~m}$ usually occupied by fir or pine-fir forests (Morón, 1990). Specimens recently collected on the Atlantic slopes of the Citlaltepetl volcano represent a new species of the lecontei group of Plusiotis. This is described here and a key to separate the species of this group is included. Lastly, the distribution of this group is briefly compared with the fir forest distribution.

## Plusiotis citlaltepetlamayatli, new species

Figs. 1, 3, 5
Description. Holotype male. Length 28.8 mm , maximum width 14.2 mm . Dorsum brilliant greenish-yellow; marginal regions of clypeus, lateral regions of pronotum, scutellum and tibiae dark pink; apical calla of elytra golden; tarsi with a reddishgreen metallic tint. Clypeus semicircular with an inconspicuous apical emargination, lateral margins slightly raised; clypeus and frons with dense punctures, becoming confluent toward apex of clypeus. Interocular distance equal to 2.4 transverse diameters of an eye. Antennal club shorter than interocular distance (0.70:1). Labrum slightly stout, medially slightly excavated, ventral border truncate and exposed (frontal view). Apex of labium broadly sinuate, with two central, effaced teeth. Pronotum with lateral borders almost evenly curved, anterior and posterior angles of pronotum rounded; pronotum margined except at central half of apical border; disc of pronotum with small and moderately dense punctures, laterally more dense. Scutellum as long as wide. Elytral striae shallow; interstriae little convex, with scarce, medium-size


Figs. 1-4. Genitalia of Plusiotis spp. 1, Aedeagus of P. citlaltepetlamayatli in ventral (left) and dorsal (right) view. 2, Aedeagus of $P$. alticola in dorsal (left) and ventral (right) view. 3, Inferior plates of $P$. citlaltepetlamayatli in distal view. 4, Inferior plates of $P$. difficilis in distal view.
punctures. Epipleural fold extending just to level of second visible abdominal sternite. Pygidium little convex, without metallic shine, with rugose punctation on base and sides, sparser towards disc and apex and with apical, scarce setae. Thoracic sternites clothed with abundant, long setae. Prosternal process semitriangular and prominent,


Fig. 5. Dorsal habitus of Plusiotis citlaltepetlamayatli.
with scarce setigerous punctures on ventral face. Mesosternal process rounded, short but distinct. $1-4$ visible abdominal sternites with scarce and small setae, last two almost glabrous; sixth sternite apically with broad emargination, medially with shallow transverse impression. Protarsi feebly thickened; femora slender with small, scarce punctures. Genitalia with parameres slightly asymmetrical, fused, sharply pointed, feebly notched at apex and slightly curved downward; ventral plates nearly symmetrical, depressed in basal three-fourths and apically rounded.

Allotype female. Length 30.1 mm ; maximum width 15.1 mm . Similar to male except as follows: Marginal regions of clypeus and lateral regions of pronotum with dark pink color extended and tibiae with same color reduced. Clypeus with apex slightly raised. Epipleural fold extending a little beyond from level of second visible sternite. Mesosternal process a little more produced. Abdominal sternites with setae scarcer, fifth abdominal sternite less emarginate, sixth sternite without transverse impression and apically rounded. Protarsi not thickened; femora stouter. Inferior genital plates very convex with mesoapical borders lateraly recurved, and with setae on apex and inner border.

Variation. Length of males is 26.1 mm to 28.2 mm and maximum width varies from 13.5 mm to 13.9 mm ; length of females is 29.9 mm to 31.4 mm and maximum width varies from 15.0 mm to 16.2 mm . Color pattern similar to that of the holotype, except for one specimen yellowish green; clypeus, scutellum and tibiae vary from pink predominant (common state) to green predominant (less common) and intensity of pink color varies from dark to clear. Labial apex varies from broadly sinuate (common state) to almost right (less common) with the 2 central teeth effaced or accentuated. Pronotal anterior angles vary from rounded (common state) to right (less common). Punctation on pronotum and elytra vary a little in density. Mesosternal process a little longer than that of holotype and parameres of male genitalia vary a little in length.

Type material. Holotype, male: MEXICO: VERACRUZ; Calcahualco Nueva Vaqueria Alt 2,560 m 20-VIII-1992 (between 18:45-21:15 hrs) G. Nogueira col. Allotype female same data as holotype, both eventually deposited in M. A. Morón collection (Xalapa, Mexico) final deposition at Instituto de Biologia UNAM (D.F., Mexico). Paratypes, nine males four females: 2 males 1 female, same data as holotype; 2 males 1 female, same data except between 5:00-6:00 hrs; 2 males same data except "perchando"; 1 male 1 female, same data except Alt $1,690 \mathrm{~m}$; 1 male, Tecoanapa Bosque Mesofilo Alt 2,400 m 24-26-VI-1992 Capistran y Delgado cols.; 1 male 1 female, Tlacotiopa, Alt 2,630 m 30-VII-1992 Capistran y Delgado cols. Paratypes are deposited in the collections of California Academy of Sciences (San Francisco), H. \& A. Howden (Ottawa), G. Nogueira (Guadalajara), M. A. Morón (Xalapa), C. Deloya (Xalapa), L. Delgado (D.F.), J. P. Beraud (Cuernavaca) and J. Blackaller (D.F.).

Etymology. The new species name, citlaltepetlamayatli, comes from the Mexican (Nahuatl) words: "Citlaltepetl" that means "the star's volcano" (name applied to the Pico de Orizaba volcano) and "mayatli" that means "beetle" in relation to the distribution of this beetle at the slopes of the Citlaltepetl volcano.

Remarks. Of the lecontei group, Plusiotis difficilis Morón (male unknown) is the species related most closely to Plusiotis citlaltepetlamayatli n. sp. However, Plusiotis difficilis presents color yellowish-green; clypeus semitriangular; labrum medially
strongly excavated and its ventral border sinuate and directed inside; distal margin of pronotum complete; scutellum wider than long; prosternal process small with long and several setae; abdominal sternites with several long setae; female inferior genital plates as in Figure 4. Plusiotis citlaltepetlamayatli presents color greenish-yellow; clypeus semicircular; labrum medially slightly excavated and its ventral border truncate and exposed; distal margin of pronotum incomplete; scutellum as long as wide; prosternal process large, prominent and with sparse setae; abdominal sternites glabrous or at most with very few short setae and female genital plates as in Figure 3. Another closely related species is Plusiotis alticola Bates which can be separated by the characters given in the following key and the shape of the male genitalia (Figs. $1-2$ ).

## KEY TO THE LECONTEI SPECIES GROUP OF PLUSIOTIS

1. Male and female with robust metafemora and metatibiae ............................ 2
$1^{\prime}$. Male with slender metafemora and metatibiae, female with slightly widened metafemora and metatibiae 6
2. Sternal coloration metallic iridescent. Pygidium with metallic shine ................. 3
$2^{\prime}$. Sternal coloration brilliant. Pygidium without metallic shine .......................... 4
3. Antennal club longer than interocular distance. Clypeus semicircular. Jalisco, Mexico, Veracruz and D.F., Mexico

Plusiotis orizabae Bates
3'. Antennal club shorter than interocular distance. Clypeus semitrapezoidal. Arizona and New Mexico, U.S.; Sonora, Chihuahua, Sinaloa and Durango, Mexico

Plusiotis lecontei Horn
4. Sides of pronotum with a dark pink stripe. Elytral punctation dense and strong. Jalisco, Mexico

Plusiotis alticola Bates
$4^{\prime}$. Sides of pronotum green. Elytral punctation sparse and very fine. Guatemala ........ 5
5. Clypeus semitrapezoidal-rounded. Pronotum with sparse and very fine punctures. Humeral calla of elytra golden ................................ . Plusiotis pehlkei Ohaus
5'. Clypeus semitrapezoidal slightly emarginated at middle. Pronotum with dense and strong punctures. Humeral calla of elytra green ................ Plusiotis centralis Morón
6. Clypeus semitrapezoidal. Sides of pronotum green, with the lateral borders angulated. Humeral calla of elytra golden. Guerrero, Mexico ........... . Plusiotis purpurata Morón
6'. Clypeus semicircular or semitrapezoidal. Sides of pronotum with a dark pink stripe and its lateral borders rounded. Humeral calla of elytra green. Jalisco, Hidalgo, Mexico
7. Clypeus semitriangular. Labrum medially strongly excavated, its ventral border sinuate and toward inside. Distal margin of pronotum complete. Prosternal process small with dense setae. Hidalgo, Mexico

Plusiotis difficilis Morón
7'. Clypeus semicircular. Labrum medially slightly excavated, its ventral border truncate and exposed. Distal margin of pronotum incomplete. Prosternal process prominent with sparse setae. Veracruz, Mexico

Plusiotis citlaltepetlamayatli sp. nov.

## DISCUSSION

The species of the lecontei group are restricted to highlands above $2,000 \mathrm{~m}$, with an isolated distribution and usually associated with fir forests or cloud and coniferous forests. They are also associated with semicold or temperate humid and subhumid climate (sensu Garcia, 1973). Of the eight recognized species only one is distributed at north of the Eje neovolcanico transversal: P. lecontei, which is distributed from
southwestern U.S. to northwest of Mexico, between 2,000-3,000 m and associated with pine-oak forests with temperate subhumid climate. Four species are only found at the Eje neovolcanico transversal: P. orizabae with an insular distribution situated at the western, central and eastern regions of this mountainous system, between $2,800-3,800 \mathrm{~m}$, associated with fir-pine or pine-fir forests with semicold or temperate subhumid climate; $P$. difficilis from the Sierra de Pachuca (Hidalgo state), between $2,500-2,750 \mathrm{~m}$ in fir-juniper forests and with semicold subhumid climate; $P$. alticola from the slopes of Volcan Nevado de Colima (Jalisco), between 2,600-3,600 m with fir-pine forests and a temperate subhumid climate; and $P$. citlaltepetlamayatli from the external slopes of the Volcan Citlaltepetl, between 2,400-2,700 m with pine-fir forests and a temperate humid climate. The remaining species are located south of Eje neovolcanico transversal: P. purpurata from the Sierra de Igualatlaco and Campo Morado (Guerrero) at the Sierra Madre del sur, between $2,000-2,800 \mathrm{~m}$ with pinefir, pine-oak and cloud forests with temperate subhumid climate; $P$. centralis only known from the type locality at Quezaltenango in Guatemala associated with pineoak forest and humid temperate climate at $2,200 \mathrm{~m}$ altitude; and $P$. pehlkei found along the Pacific escarpment of the northwestern end of the Guatemalan highlands, between 2,100-2,350 m with pine-oak forests (the last two species are located in areas below the Guatemalan fir-forests) (Morón, 1990). Distribution of the lecontei group and Mexican Abies species show great similarities. Both have their southern limit at the northwestern highlands of Guatemala; most of the species are primarily found between $2,400-3,600 \mathrm{~m}$, at zones with high humidity with annual rainfall above $1,000 \mathrm{~mm}$ and with temperate or semicold conditions. Several species are distributed at the Eje neovolcanico transversal, fewer at the mountainous systems of the south and scarcely at the Western Sierra Madre; furthermore 75\% (six species) of Mexican Abies and $83 \%$ (five species) of the Mexican species of the lecontei group are endemic to this country, and this jointly with their isolated distribution confers on them a relictual character (Rzedowski, 1978; Morón, 1990, 1991).

Based on this information, we suggest that the ancestral lineage of the lecontei group has dispersed through a corridor of fir or pine-fir forests, during its expansion to the Mexican mountains. This hypothesis is supported by the presence of fossil evidence of the genus Abies from Late Cretaceous at Coahuila State and from Miocene at Tehuantepec Isthmus (Rueda-Gaxiola, 1967 and Graham, 1972; cited by Rzedowski, 1978), which suggest the existence of adequate forest-zones for dispersal and posterior diversification of the lecontei group which since its origins could be associated with temperate conifer forests, with fir as the dominant or co-dominant tree. In contrast the adelaida group is also associated with temperate conifer forests with pine as the dominant tree, at lower altitudes and drier conditions than those of the lecontei group, so, continuous distribution of the pine or pine-oak forests prevents isolation of the adelaida group, which actually comprises only three species with wide distribution. It is likely that the climatic conditions have been a decisive factor in the dispersal and diversification process of some species groups.

Finally, Mexican fir forests occupy only $0.16 \%$ of national territory (Rzedowski, 1978) and are constantly being destroyed by mankind's activities. These problems and its low ecological tolerance to other habitats lead us to conclude that at least five species of lecontei group are in danger of extinction: P. alticola, P. orizabae, P. difficilis,
$P$. purpurata and $P$. citlaltepetlamayatli (we do not consider the other Mexican species because of its wide distribution).

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# TWO NEW FLAT BUG SPECIES FROM NORTH AMERICA (HETEROPTERA: ARADIDAE) 

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Abstract.-Two new North American species (Aradus froeschneri and Neuroctenus unistel-
latus) are described.

During my stay in the United States, through the ICOM/AAM International Partnership Amongst Museums program, I had the possibility to study the collections of the National Museum of Natural History, Washington, and the American Museum of Natural History, New York, and to collect some flat bug species. In the course of investigations some new species were found, of which two are described here.

## Aradus froeschneri, new species

Figs. 1-5
Macropterous, brownish, tip of antennal joint 2, 3, 4, head, anterior lobe of pronotum, basis of scutellum and legs dark brown, partly with yellowish granulation.

Head 1.2 times as long as wide across eyes (Fig. 1). Anterior process robust, reaching beyond $1 / 4$ of antennal joint 2 . Antenna long, joint 2 thickening towards apex, 3 and 4 cylindrical, subequal in length. Antennal formula 10:54:18:18. Antenniferous tubercle strong, pointed, lateral tooth blunt. Postocular tubercle with strong, transversely directed apical tubercle (granule). Rostrum reaching near to hind margin of mesosternum.

Pronotum more than 2 times as wide as long, widest beyond middle. Fore disc strongly convex, with white granules medially and laterally and smooth between them and the carinae. Hind disc rising posteriorly. Lateral margin reflexed, more steep anteriorly, with large teeth decreasing in size towards rounded PE angles.

Scutellum lacking apical half. Basal part elevated, with yellow and reddish granulation, margins reflexed, parallel.

Hemelytra light brown, basal dilation moderate, reflexed (Fig. 2).
Abdomen oval, PE angles of dorsolaterotergites (DLTGs) sharply rounded, slightly protruding. Tip of abdomen on Figure 3.

Male genitalia: Tergite 9 comprising two lobes both positioned subvertically, the anterior one thin, transparent (Fig. 4). Paramere broad, large, with longish, narrowing apex posteriorly and small tooth directed anteriorly. Parandrium about the same in height along the whole length (Fig. 5).

Measurements: total length of body about 8.5 mm , length of head 1.58 mm , width of head 1.33 mm , length of pronotum 1.2 mm , width of pronotum 2.6 mm , width of scutellum 1.2 mm , maximum width of abdomen 3.7 mm .

Holotype, male, damaged, but critical body parts present (only tip of scutellum missing): "Pinehurst, Calif. III. 27. '34.," "R. L. Usinger collection," "collection N.


Figs. 1-8. $\quad 1-5=$ Aradus froeschneri sp. n., $6=$ A. inornatus Uhler, $7=A$. acutus Say, $8=$ A. blaisdelli Van Duzee, $1=$ head and pronotum, $2=$ hemelytra, $3=$ tip of male abdomen, 4 $=$ tergite $9,5-8=$ parandia.

Kormilev," "Aradus blaisdelli VD. det R. L. Usinger '49," "C. J. Drake collection 1956." Deposited in the National Museum of Natural History, Washington.

The species is dedicated to Dr. R. C. Froeschner, Curator of Hemiptera in the NMNH and excellent contributor to our knowledge of Aradidae.

In spite of the fact that the new species runs in the key of Torre-Bueno (1939) to, and the sole specimen was identified as $A$. blaisdelli, considering other body characters than the long second antennal joint, it is more closely allied to A. acutus Say. The new species can be distinguished from three related species, blaisdelli Van Duzee, acutus Say and inornatus Uhler, besides measurements and other features, by the shape of the parandrium (Figs. 6-8), or the shape of tergite 9 being bilobate in all species of the acutus species group but the two lobes more dorsoventrally flattened ("horizontally") in the afore mentioned three. It differs from paganicus Parshley, respectively, by several features. Antennal formula is 12:54:18:16 in paganicus, rostrum reaches to the middle of mesosternum, ratio of width of head to length of pronotum is different (28:30), margin of pronotum is more serrate, etc.

It should be mentioned here, that the drawings of Matsuda (1977) of $A$. paganicus contradict the photographs. A revision of the species of the acutus-group (betulaegroup in the Old World) seems to be necessary.


Figs. 9-16. $9-15=$ Neuroctenus unistellatus sp. n., $16=$ N. simplex Kormilev, $9=$ total drawing of adult male, $10=$ antenna, $11,16=$ paramer in situ, $12=$ tip of abdomen of female, $13=$ head and pronotum of fourth instar larva, $14=$ same, tip of abdomen, $15=$ total drawing of fifth instar larva.

## Neuroctenus unistellatus, new species

(Figs. 9-15)
Macropterous (Fig. 9), nearly unicolorous dark brown, base of membrane whitish.
Head about as long as wide. Anterior process reaching beyond tip of antennal joint 1. Antenniferous tubercle strong, pointed, lateral borders diverging. Antennal joint 1 and 2 club shaped, 3 subcylindrical, 4 spindle form (Fig. 10). Antennal formula: 25:25:27:23 (male), 25:25:28:22 (female). Infraocular carina distinct, low. Postocular tubercle in most cases pointed and reaching beyond outer border of eyes. Vertex slightly convex, evenly covered with granules.

Pronotum trapezoidal, 2.3-2.4 times as wide as long. Anterolateral angles rounded. Disc with 2 shiny callous spots and with 1 mediolateral and 1 lateral depression on each side, separating fore and hind disc. PE angles sharply rounded, produced posteriorly, wrinkled under granulation.

Scutellum triangular, 1.4 times as wide as long. Lateral margin slightly arched, concave, elevated except at the tip. Disc with transverse wrinkles along median line on the posterior $2 / 3$.

Abdomen oval. PE angles of DLTGs slightly protruding against anterior angles of the next DLTG. DLTG 3-6 with distinct sublateral, longitudinal carina on females, sometimes with signs of such on males.

Genitalia: Tip of abdomen depicted on Figures 9 and 11. Parameres in situ also figured (Fig. 15).

Larvae: only fourth (Figs. 13-14) and fifth (Fig. 15) instar larvae available. They are yellowish white with brown rows of apodemal impressions. Length is about 3 mm in the fourth and 4 mm in the fifth instar. Head is 1.45 times as wide as long on the fourth and 1.2 times as wide as long on the fifth instar. Antennal formula is 20:25:25:30 for the fourth and 20:23:29:28 for the fifth instar. They fit into the picture drawn for the postembryonal development of Neuroctenus (Vásárhelyi, 1988) including changes in the antennal formula, in the development of sclerites on the head, pronotum and the tip of abdomen (Figs. 13-15).

Measurements (averages of 3-3 specimens, first the male then the female data are given): total length of body $4.1-4.4 \mathrm{~mm}$, length of head $0.7-0.72 \mathrm{~mm}$, width of head 0.7 mm , length of pronotum $0.57-0.58 \mathrm{~mm}$, width of pronotum $1.33-1.40 \mathrm{~mm}$, length of scutellum $0.63-0.68 \mathrm{~mm}$, width of scutellum $0.88-0.93 \mathrm{~mm}$, maximum width of abdomen across segment 5 and 4 respectively $1.83-1.93 \mathrm{~mm}$.

Holotype (male) and paratypes ( 15 males, 12 females, 11 larvae): USA, Texas, Austin, Brakenridge Field Lab., 550 ft ." "10. 05. 1991. leg T. Vásárhelyi and C. R. Nelson." One male and one female deposited in each of the National Museum of Natural History (Washington) and in the American Museum of Natural History (New York), the holotype male and 12 males, 10 females and 11 larvae deposited in the Hungarian Natural History Museum, Budapest.
Natural History Museum, Budapest.
It is a pleasure to dedicate this new species to the "Lone Star State" and its helpful and friendly citizens.

The new species cannot be identified by the key of Torre-Bueno (1939), because the apex of head is distinclty cleft on many specimens but is not distinctly cleft on some. Scutellum with traces of a faint median carina apically, i.e., transversely rugose posteriorly. Abdomen is broadly oval. This character set separates it from all other species included in the key. The new species is closely allied to both $N$. rossi Kormilev and $N$. simplex Kormilev. In rossi the antenna is thicker, with joint 1 surpassing tip of anterior process of head, anterolateral border of pronotum cut out in an obtuse angle, and the sclerite bearing the mediolateral apodemal impressions is much narrower. In simplex antennal joint 4 is relatively longer, the anterolateral border of pronotum straight or slightly concave, the apical border of corium bisinuate, the wings are not bordered by carinae on the abdomen of the male, and the tip of abdomen is different (Fig. 16).

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# TAXONOMY AND DISTRIBUTION OF THE HOLARCTIC DIVING BEETLE LACCOPHILUS BIGUTTATUS KIRBY (COLEOPTERA: DYTISCIDAE) 

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#### Abstract

Several authors suggest that the Palearctic Laccophilus minutus (Linneaus 1758) and the Nearctic L. biguttatus Kirby 1837 are synonymous. Our investigation confirmed the opinion of other authors that they refer to separate species. However, L. biguttatus is Holarctic and L. strohmi Thomson 1874 (Halsingland, Sweden) and L. apicicornis Reitter 1899 (northern Mongolia) are junior subjective synonyms (NEW SYNONYMIES). Available specimen data suggest that L. biguttatus has two centers of abundance: western North America and Mongolia + adjacent Russia.


This paper is part of a series of papers investigating taxonomic relationships of Holarctic species of Dytiscidae. These papers have grown out of the simple question: How many species of Dytiscidae are shared between the Palearctic and Nearctic regions? An unpublished list compiled from other publications showed in excess of 100 names of dytiscids are mentioned by one or more authors as having a Holarctic distribution. This investigation began with an exchange of specimens and convinced us that examination of type material was critical to the project and that some concepts of Nearctic and Palearctic species needed modification or adjustment. Interestingly many of the synonymies discovered were not on our original lists of potentially Holarctic species. Earlier papers in this series are Nilsson (1981a, b, 1983a), Roughley and Pengelly (1982), Larson and Roughley (1983), Nilsson and Larson (1984) and Larson and Nilsson (1985). The latter three references enumerate the major reasons for the taxonomic problems and we presently add to this list problems which can be solved by thorough and careful examination of type specimens as well as accurate and detailed characterization of the species involved.

Various authors (e.g., Zimmerman, 1970) have noted the similarity between the Palearctic species Laccophilus minutus (Linnaeus 1758) and the Nearctic species L. biguttatus Kirby 1837. Examination of reliably determined specimens of each taxon convinced us that these were indeed distinct species. However, for the sake of completeness, we decided to examine specimens of other Palearctic taxa to determine if other names might apply to this species. We discovered the synonymy proposed below. Furthermore, the scope of many of the problems of the taxonomy of Holarctic species are well illustrated by the example of L. biguttatus Kirby.

## HISTORICAL REVIEW

The taxonomic history of this species is relatively long and complex. Laccophilus biguttatus Kirby was described in 1837 and is the oldest available name. Kirby did
not specify a type locality for his specimen but it is inferred to be "Boreal America" because Kirby's original description appeared in Richardson's Fauna Boreali-Americana. This work was quite inaccessible in North America and prompted Bethune's ( $1871: 30$ ) quotation of the original work. Presumably because of this and because of a lack of specimens for comparison, the leading North American coleopterists of their time, J. L. LeConte and G. H. Horn considered L. biguttatus as conspecific with one or two of the more common and better known species of the eastern Nearctic region. Even after access to the original description, Horn (1883:282) was not convinced that this taxon was in the correct genus when he stated ". . . This has been placed as a synonym of two other species at various times, but it is probably not a Laccophilus at all and seems to be a species of Hydroporus, perhaps allied to pulcher Lec." Horn (1883:281) stated that he had seen the types of almost all of Kirby's species, however it is doubtful that he had seen the type of L. biguttatus because of his statement.
C. G. Thomson described L. ströhmi from Helsingland, Sweden in 1874 and L. apicicornis Reitter 1899, was described from northern Mongolia. Thomson's and Reitter's concepts were similarly inadequately understood by the leading European coleopterists. For example, Sharp (1882:821) treated L. strohmi as incertae sedis commenting that it might be a variety of L. interruptus Panzer [now known as $L$. hyalinus (DeGeer)]. Sharp (1882:289), on the other hand, treated L. biguttatus as a junior synonym of the Nearctic species, L. proximus Say, signified by use of the annotation "M.C." for the Munich Catalogue of Gemminger and Harold (1868) as a reference to this synonymy. It is curious that Sharp did not study Kirby's types lodged in the British Museum. It is clear from comments in some of Horn's and LeConte's papers that they fully expected Sharp would provide authoritative judgement on the status of Kirby's species, however, this was not done.

Fall (1917) described L. inconspicuus from Winnipeg, Manitoba, Canada and this may well have been due to Sharp's failure to mention L. biguttatus explicitly. Fall's name was the one used in North America until Balfour-Browne (1944) made it a junior synonym of Kirby's name after examination of Kirby's type specimen. In the Palearctic region distribution was slowly becoming the most widely used taxonomic character to distinguish between L. strohmi and L. apicicornis. However as the known ranges of these "species-names" extended more confusion resulted. For instance, from the Jakutsk region, Russia, Poppius (1905) listed the occurrence of L. obscurus var. stroehmi and five years later Zaitzev (1910) listed the name L. apicicornis for specimens from the same area.

Zimmermann (1930) treated L. strohmi as a variety of L. minutus and members were characterized as differing from the typical form in color and microreticulation. The same character states were used by Zimmermann for the separation of L. apicicornis and L. minutus. Gschwendtner (1939:23) discussed a variety of L. minutus from Swedish Lapland. Our subsequent examination of this specimen convinced us that it belongs to L. biguttatus.

Brinck (1942) first surmised that L. strohmi and L. apicicornis were closely related but he did not provide characters by which they could be separated. He conclusively demonstrated that L. strohmi was distinct from L. minutus in body shape, color, elytral sculpture and shape of the median lobe.

Zimmerman (1970) revised the Nearctic members of the genus Laccophilus. He
noted the similarity between $L$. minutus and $L$. biguttatus and suggested that the two may be conspecific. In his monograph, Zimmerman used some of the same character states as had Palearctic workers earlier; however, he assigned them differing levels of taxonomic value. For instance his statement (1970:194) that members of these two taxa are similar in sculpture is ambiguous. Adults of L. minutus have a finely impressed secondary reticulation as well as primary reticulation whereas specimens of L. biguttatus have only primary reticulation. Therefore Zimmerman must have negated such differences in sculpture as of low taxonomic value. In contrast, character states of elytral reticulation are interpreted as being of high taxonomic value by Brancucci (1983) in his revision of Laccophilus from the eastern Palearctic, Oriental and Australian regions and by other European taxonomists. Brancucci also discussed the similarity between L. minutus and L. biguttatus (as L. apicicornis) but maintained them as specifically distinct and assigned them to separate species groups of Laccophilus, based in part on differences of elytral sculpture.

The synonymy of L. biguttatus may not yet be complete. Feng (1937) described L. uniformis Feng based on two female specimens from Shan Hai Koan, Hopei, China. This name is preoccupied and Guignot (1942) has supplied the replacement name, L. fengi. This species is certainly very close to L. biguttatus, however, efforts by Brancucci (1983) and ourselves have failed to locate the type series.

## TAXONOMY

## Laccophilus biguttatus Kirby, 1837

Laccophilus biguttatus Kirby, 1837:69; Bethune, 1871:30; Horn, 1883:282; BalfourBrowne, 1944:345; Gordon and Post, 1965:12; Zimmermann, 1970:193; Larson, 1975:260.
Laccophilus americanus, ex parte, LeConte, 1850:214; Branden, 1885:20; nec Aubé, 1838.

Laccophilus proximus, ex parte, Melsheimer, 1853:31; Gemminger and Harold, 1868: 445; LeConte, 1870:398; Horn, 1872:127; Horn, 1876:150; Sharp, 1882:289; Zimmermann, 1920:25; nec Say, 1823.
Laccophilus ströhmi Thomson, 1874:535. NEW SYNONYMY. Thomson, 1885:18; Sahlberg, 1886:206; Sahlberg, 1900:14; Brinck, 1942:123; Lindroth, 1960:148; Charpentier, 1972:291.
Laccophilus interruptus var. stroehmi, Sharp, 1882:281; Branden, 1885:22.
Laccophilus apicicornis Reitter, 1899:198. NEW SYNONYMY. (see citations in Brancucci, 1983:283).
Laccophilus n. sp., Wallis, 1915:170.
Laccophilus inconspicuus Fall, 1917:164; Wallis and Larson, 1973:101.
Laccophilus minutus var. ströhmi, Guignot, 1931:508.
Laccophilus stroehmi, Strand, 1970:119; Silfverberg, 1979:6; Nilsson, 1983b:9; Hagenlund, 1984:104.

Diagnosis. Color varied, dorsal surface testaceous to pale brown and venter pale yellowish-brown to nearly all black. Elytra without distinct color pattern and with microsculpture single, luster rather dull. Antennae slightly thickened and with last seven segments darkened apically. Male without stridulatory file. Total body length 3.9 to 5.0 mm . Median lobe of aedeagus as in Figures 1-6.


Fig. 1-6. Left and right lateral views of median lobe of aedeagus of male specimens of Laccophilus biguttatus Kirby ( 1 \& 6, Canada, 2 \& 5, Mongolia, 3 \& 4, Norway).

Zimmerman (1970) gives a very good description of L. biguttatus and compares it to other Nearctic species. Brinck (1942) gives characters for its recognition in Europe (as L. strohmi), and, as L. apicicornis, it is well described and compared to members of the eastern Palearctic fauna by Brancucci (1983).

Notes about type material. The single specimen of L. biguttatus which Kirby examined is from North America and is deposited in BM [museum abbreviations follow Brancucci (1983:243-244), others are given in acknowledgments]. The holotype is a male and is labelled as follows: "Type/H.T./577la, N. Amer. (on underside of label)/ N. American/Laccophilus biguttatus Type Kirby."

The lectotype female of L. ströhmi Thomson (here designated by A.N.) is from Sweden and is labelled "Hsl. Str." and lectotype label. Paralectotype (here designated by AN.) labelled "Norl" and paralectotype label. Eight additional specimens were studied from C. G. Thomson's collection in UML.

The holotype of L. inconspicuus Fall, deposited in MCZ, is labelled "Winnipeg, vi-3-11/Type, inconspicuus/M.C.Z., Type, 23885/H.C. Fall, Collection." Details concerning the types of L. apicicornis Reitter, which is from northern Mongolia and deposited in BU are provided by Brancucci (1983:284). The latter were also examined by the junior author.

Material examined. All known locality records are mapped on Figure 7. Too many specimens from the Nearctic region were examined to list here. The following specimens were seen from Palearctic localities (arranged by country from west to east). NORWAY: Aay, Gjerstad, Heilandsvann, 13 \& 29.v.1983, G. Hagenlund (10, AN). SWEDEN: Bohuslän, Spekeröd, 14.v.1984, B. Andrén (7, AN). Hälsingland, Ströhm (6, MNHG, 10, UML, 1, UZM). Jämtland, Ströhm (1, MNHG). Lule lappmark, Jokkmokk, Gschwendtner (1, OLM) Norrland, C. G. Thomson (1, UZM). Torne lappmark, Sappisaasi, 16.vii.1966, T. Karlsson (1, UML).
FINLAND: Kl, Jaakkaima, J. Sahlberg (1, UZM). Ok, Säräisneimi, 16.viii. 1947, Håkan Lindberg (11, UZM). Ob, Turtola, J. Sahlberg (1, UZM).


Fig. 7. Distribution of Laccophilus biguttatus Kirby, locality records from specimens examined and literature.

RUSSIA: Russian SFSR, Leusch [=Leuši], Sundman (1, UZM). Samarovo [=HantyMansijsk], (2, UZM). Tobolsk, Granö (2, UZM). Verchojansk, v \& vi 1885, Bunge and Tol (3, ZIL). MONGOLIA: Changai, Leder (holotype and 3 paratypes, BU). Mongol. b., Uaga (1, ZIL), [locality not found]. Archangaj aimak, NO Ecke des Sees Ogij nur, 1,350 m, 2.vii.1964, Exp. Dr. Z. Kaszab, Nr. 249 (3, BU). Gobi Altaj aimak, ca. 30 km SO von Somon Zargalan, Fluss Zavchan gol, 1,700 m, 16.vii.1966, Exp. Dr. Z. Kaszab, Nr. 699 (2, BU).

Structural variation. Zimmerman (1970) and Larson (1975) discussed variation in color and size of this species based on North American specimens. We examined too few specimens from the Palearctic region to be able to generalize about color variation for this area. Adult specimens vary markedly in size. Zimmerman (1970) provided a range of total length for Nearctic specimens from 3.9 to 4.8 mm with smaller specimens being more common at the northern and southeastern limits of the range. All Palearctic specimens examined were within this size range. Mongolian specimens were between 4.2 and 4.6 mm whereas Scandinavian specimens are $4.2-$ 4.8 mm . Interpopulation differences may be extensive however. Samples from Heilandsvann, Norway have a mean total length (MTL) of $4.68 \mathrm{~mm}(\mathrm{~N}=10)$ while a sample from Spekeröd, Sweden which is only 250 km distant has an MTL of 4.35 $(\mathrm{N}=7)$. Because of such interpopulation variation we have not been able to document any meaningful geographic pattern of variation. The ratio of MTL/MMW (mean maximum width), however, is about 1.8 for all samples measured.

The most notable variation of structure is in form of the median lobe of the aedeagus of male specimens (Figs. 1-6). Across North America, specimens (Figs. 1 and 4) are relatively consistent in form of the apex of the median lobe, the tip of which is a uniform extension of the pre-apical portion of the median lobe and is not differentiated. Most Siberian specimens of this species have a similar form of median lobe (see Brancucci 1983:417, figs. 153-154). In contrast, Mongolian specimens of $L$. biguttatus have the apex somewhat twisted (Figs. 2 and 4). In Scandinavian specimens the degree of torsion of the apex is greatest and therefore the undersurface of the tip of the median lobe can be seen in lateral view (Fig. 3) and the tip is therefore comparatively more differentiated (Fig. 6). While there are still large distributional gaps, we believe that the above variation is clinal and representative of separation of populations rather than species. Further study of specimens from intervening areas will support or deny our hypothesis.

Immature stages. Watts (1970) provided a short description of the third stage larva taken from acidic marshes at Delta, Manitoba. He described them as common in summer. Barman (1972) provided further details of life history and of third stage larvae from North America. Recently, Hagenlund and Nilsson (1985) have presented a detailed study of life history and immature stages in southern Norway.

## DISTRIBUTION AND ABUNDANCE

The known distribution of L. biguttatus is shown in Figure 7. Records for localities are taken from Brancucci (1983), Guéorguiev (1965, 1968a, b, 1969, 1972), Larson (1975) and Zimmerman (1970) as well as the specimens listed above. Further Nearctic locality data are from CARR, CAS, CNC, CAS and JBWM. The following notes on
abundance and distribution are based primarily on field work in North America, on what can be inferred from specimen collection data, and from previous publications.

Several authors have discussed aspects of geographic distribution and abundance, in general and over entire species ranges (e.g., Preston, 1962; Hengeveld and Haech, 1982 and Brown, 1984, and references therein). In summary, species tend to be more abundant towards the geographic center of their ranges and less common at the periphery. Brown (1984) has suggested an explanation for non-normal distribution/ abundance patterns and in particular bi- or multimodal patterns. We interpret $L$. biguttatus to have the latter type of pattern. There are three major centers of distribution based on locality information (Fig. 7): (1) Fennoscandia, (2) eastern Palearctic, in and around Mongolia, and (3) a transcontinental Nearctic component.

Most studies of distribution and abundance are based on precise sampling programs. Obviously we do not have such detail and accuracy in this case. Nevertheless it does seem profitable to analyze the known distribution of L. biguttatus. In the following discussion, we assume that there is a correlation between locality records (dots on Fig. 7), history and intensity of collecting (hereafter called collecting effort) and abundance. We believe that a relatively long history and intensity of collecting effort which results in few locality records is an indication of low abundance and low collecting effort which results in numerous locality records is indicative of increased abundance.

As noted above Fennoscandian records are geographically and temporally diffuse. The only record of large numbers of specimens is that of Hagenlund and Nilsson (1985). Therefore this "center"' is probably due more to intensive collecting of populations on the edge of the range. We fully expect that additional records of $L$. biguttatus will better connect centers 1 and 2 . The Mongolian group of localities (center 2) probably is much more indicative of abundance considering the comparatively reduced effort of collection. The majority of these records have resulted from Dr. Z. Kaszab's few expeditions to Mongolia and we interpret this as an indication of greater abundance of L. biguttatus in area 2. In North America, the distribution of dots on the map suggests that this species may be relatively abundant throughout much of the northern portion of the continent. However, in North America the total cumulative effort of collecting is very biased toward the northeastern United States and adjacent southeastern Canada. Therefore some further discussion of the Nearctic distribution is required.

In the Prairie Provinces of western Canada there are three major physiographic zones which may be broadly defined as (south to north) grasslands of the Great Plains, aspen parkland (mixture of grassland with Populus spp., etc.) and boreal forest. In this area specimens of L. biguttatus do occur sporadically on the grasslands, but are more commonly collected in parkland and forest habitats (Larson, 1975, 1985). For instance, Larson (1975) examined more than 600 specimens from the Province of Alberta where L. biguttatus was the second most frequently collected species (Larson, 1985) in his intensive study. In conjunction with its abundance this species occurred in a remarkable range of habitats and at a wide range of elevations. In increasing order of frequency of occurrence this species is known to inhabit: foothill marshes, saline ponds, warm streams and lakes, temporary grassland ponds, sphagnum bogs, boreal marshes and permanent grassland ponds (Larson, 1985). In addition, it can be found frequently in virtually any temporary site in the spring of the year (e.g.,
snowmelt puddles on sidewalks) which may indicate that this species exploits a range of temporary habitats during spring dispersal. Southward and eastward in North America this species is increasingly less commonly collected and apparently becomes restricted to habitats at higher elevations (Barman, 1972; Fall, 1917; Zimmerman, 1970). Similarly, this species is not known to as readily colonize temporary habitats towards the edges of its Nearctic range. For instance, the senior author has collected L. biguttatus at sporadic permanent habitats in southern Ontario, however this species was not found in the intensive studies of temporary ponds by Wiggins et al. (1980). James (1970) recorded this species from vernal woodland pools in Ontario but the abundance (James 1967) was notably reduced. In Ontario, at least, this species does not use temporary habitats to the same degree as in western Canada.

The range of habitats in which L. biguttatus has been collected in Mongolia is provided by Guéorguiev ( $1965,1968 \mathrm{a}, \mathrm{b}, 1969$ ). The altitudinal range is from 700 to $1,700 \mathrm{~m}$ and members of this species occurred in temporary saline ponds as well as more permanent ponds in a forest. In Mongolia, L. biguttatus is apparently common in more saline habitats and along river margins; however, in general, the habitats are similar to the range of habitats known for Nearctic populations.

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# ARADUS PERICARTI, A NEW SPECIES FROM SOUTH AMERICA (HETEROPTERA, ARADIDAE) 

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#### Abstract

A new species of neotropical Aradus is described from Surinam. Habitus, male genitalic and other structures are illustrated. A key is given for the six South American species of Aradus with bicolored antennae and their antennae are figured.


The genus Aradus shows a preponderantly Holarctic distribution and is represented in the Nearctic Region by 78 species, but only 10 are known to date from the Neotropical Region (Kormilev and Froeschner, 1987:11). Most of them belong to the "falleni" species group which is characterized by a caudoventral opening of the male genital segment VIII and bicolored antennae. All of them seem to be rare in collections although they are good flyers and mostly collected at light. Their biology and ecology are still unknown.

Specimens from Surinam proved to belong to a new taxon which is described below. To ascertain the identity of neotropical species described by Stal in the last century it was necessary to revise his type material. A paper with the results of the type-investigation is in press.

## Aradus pericarti, new species

(Figs. 1-3, 9-19)
Diagnosis. Distinguished from all neotropical members of the falleni species group by its shape and coloration of the antennae and the male genitalic structures shown in Figures 9-19.

Description. Male. Macropterous; body elongate, its surface and appendages covered with fine granulation which partially bears short bristles.

Head. Shorter than width across eyes (33/37); clypeus constricted at middle, apex rounded. Antenniferous tubercles reaching $1 / 2$ of antennal segment I, apices acute. Eyes large, globose. Preocular tubercles distinct, blunt. Postocular portion of head rounded, strongly converging posteriorly, without postocular tubercles. Vertex granulate medially with $2(1+1)$ smooth, oval depressions laterad, posteriorly delimited by a thin v-shaped whitish transverse callosity.

Antennae. $1.59 \times$ as long as width of head across eyes; segment I subcylindrical, segments II to IV depressed; II constricted at base, apically enlarged and with parallel sides as segments III and IV. Rostrum arising from an open atrium, reaching $3 / 4$ of prosternum.

Pronotum. $1.75 \times$ wider than long (58/33); lateral margins straight and converging anteriorly, anterolateral lobes angulately rounded, anterior margin dentate laterally. Disk with 4 longitudinal carinae and carinate humeri.

Scutellum. Triangular with elevated lateral margins, disk raised at basal 1/3.


Figs. 1-8. 1-3. Aradus pericarti, new species. 1. Habitus of male holotype. 1a. Lateral view of right antenna. 2. Female, venter. 3. Female, abdomen dorsal. 4-8. Antennae of neotropical Aradus. 4. penningtoni. 5. brasiliensis. 6. falleni. 7. fronterana. 8. mexicanus. Scale 0.5 mm .

Abdomen. Lateral margins straight, slightly converging anteriorly. Hemelytra complete, corium reaching anterior border of dorsal laterotergite (dltg) VI; membrane hyaline with distinct veins. Spiracles II to VII ventral, VIII dorso-lateral and visible from above.
Genitalic structures. Genital segment VIII cup-like with expanded and raised posterior lobes and a caudoventral oval opening (Figs. 12-14). Pygophore globose, flattened dorsally (Fig. 9). Parandria as Figure 19; parameres as Figures 15-18; tergite


Figs. 9-19. Aradus pericarti, new species. 9. Pygophore dorsal. 10. Left lobe of tergite IX dorsal. 11. Dto. lateral. 12. Male genital segment VIII lateral. 13. Dto. dorsal. 14. Dto. caudal. 15-18. Left paramere in different positions. 19. Parandrium lateral. Scale 0.2 mm for Figure $9,0.5 \mathrm{~mm}$ for Figures $12-14,0.1 \mathrm{~mm}$ for Figures $10,11,15-19$.

IX formed by $2(1+1)$ lobes with acute apices which are curved downwards (Figs. 10, 11).

Legs. Slender. Trochanters of fore- and middle legs fused, those of hind legs marked by a distinct suture.

Female. Similar to male but larger and abdomen more rounded laterally. Paratergites VIII as Figures 2, 3.

Coloration. Generally dark brown to black, but legs are usually of lighter color. Whitish-yellow are the median portion of antennal segment II, segment III except the base and the posterior-exterior angles of dltg III to VII on dorsal and ventral side.

Etymology. Dedicated to my friend and eminent French heteropterist Mr. Jean Péricart, in occasion of his 65th birthday.

Holotype. Male, Surinam, Marowijne Prov., Oelemari River, Oct. 88 lg. Vincenti, in coll. EH.

Paratypes. 2 ôô, 3 ọ collected with holotype in coll. EH, a paratype will be deposited in USNM, Washington.

Measurements. Holotype $\delta$ : Length 4.8 mm ; width of abdomen across corium 1.52 mm . Paratypes 99 : Length $5.15,5.25,5.55 \mathrm{~mm}$; respective width across corium 1.72, $1.73,1.85 \mathrm{~mm}$, across tergite IV 2.2, 2.2, 2.37 mm . Relative length of antennal segments basically as in males.

## DISCUSSION

The South American Aradus fauna comprises 5 species with bicolored antennae, but mexicanus, Usinger 1936, which is also found in Brazil, lacks the caudoventral opening of the male genital segment VIII. A. fronterana Drake, 1942, was also described from Mexico but occurs possibly in Northern South America and is therefore included in the key. It might have been confused with the widespread falleni Stal, 1860. These 6 species can be separated by the following key:

## KEY TO SOUTH AMERICAN ARADUS WITH BICOLORED ANTENNAE

1 (2) Antennal segment II with apical $1 / 5$ whitish, basal $1 / 4$ of III dark, IV whitish (Fig. 8), male segment VIII without a caudoventral opening .......... mexicanus Usinger

2 (1) Whole antennal segment II dark (Figs. 4, 5) or predominantly yellowish (Figs. 1,

3 (6) Antennal segment II entirely dark .................................................... . 4
4 (5) Only antennal segment III yellowish (Fig. 4) ..................... . penningtoni Drake
5 (4) Antennal segment III and basal half of IV yellowish (Fig. 5) ......brasiliensis Usinger
6 (3) Antennal segment II predominantly yellowish (Figs. 1, 6, 7)
7 (8) Antennal segment II depressed, its basal and apical $1 / 4$ dark, III yellowish with dark

8 (7) Antennal segment II not depressed, coloration of antennae different ............. 9
9 (10) Antennae yellowish to brown, usually segment I, basal $1 / 4$ of II and III darker, segment II constricted at base (Fig. 6) ..................................... falleni Stal
10 (9) Antennae yellowish with segment I, basal $1 / 4$ of II, base of III and apical $1 / 3$ of IV dark, segment II longer and evenly tapering towards base (Fig. 7) . . fronterana Drake

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# THE FIRST RECORD OF EREMOCHILINI (COLEOPTERA: COCCINELLIDAE: EPILACHNINAE) FROM MEXICO 

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#### Abstract

Eremochilus howdeni, a new species of the plant feeding subfamily Epilachninae, is described and figured, and a new key to species of Eremochilus is presented. Additions and modifications are made to the original generic description.


A revision of the subfamily Epilachninae by Gordon (1976) recognized 2 tribes, Epilachnini and Madaini. Subsequently Eremochilini was erected for the aberrant neotropical genus Eremochilus (Gordon and Vandenberg, 1987) from Bolivia and southern Brazil. Examination of unidentified Coccinellidae in the Canadian National Collection resulted in discovery of an undescribed Eremochilus from Sinaloa, Mexico. If this occurrence represents a tremendous range extension rather than simply a disjunction, we may anticipate both the existence of additional species and perhaps a much broader distribution of each species than is now known. The scarcity of collected specimens is unusual in a taxon of this plant feeding subfamily. The cylindrical body form and extremely modified mouthparts lead one to speculate that it might feed "internally" rather than on leaf surfaces, e.g., in rolled leaves or perhaps even in stems. The latter possibility would account for the scarcity of specimens.

Characters not included in the original generic description are: terminal segment of maxillary palpus short, slightly securiform (Fig. 4), labial palpus slender, terminal segment $1 / 2$ length of preceding segment (Fig. 5), closeup view (Fig. 6); subgena produced forward nearly to clypeal apex (Fig. 3); base of mandible sinuate (Fig. 2), apex of mandible with 3 blunt teeth (Figs. 2, 3).

Type specimens are deposited in the Canadian National Collection, Ottawa, Ontario (CNC) and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

## REVISED KEY TO SPECIES OF EREMOCHILUS

1. Clypeal apex emarginate; Bolivia . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . peregrinus Weise

Clypeal apex truncate; Brazil, Mexico 2

2(1). Abdominal sterna 2-4 each with transverse rugae medially in basal $1 / 3$; front of head flat between eyes; Brazil . . . . . . . . . . . . . . . . . . . . . . . . . . . weisei Gordon and Vandenberg Abdominal sterna 2-4 smooth, punctate medially in basal $1 / 3$, without rugae; front of head convex between eyes; Mexico howdeni, n. sp.


Figs. 1-6. Head structures. Fig. 1, frontal view of head; 2, mandibles, oblique view; 3, mandibular apex, subgena; 4, maxillary palpus; 5 , labial palpus; 6 , terminal segment of labial palpus.

## Eremochilus howdeni, new species

Description: Length 3.5 mm , width 2.20 mm . Form elongate, nearly parallel sided, widest at middle of elytra, strongly convex in lateral view. Color yellowish brown throughout except mandibles dark reddish brown, remainder of mouthparts, antenna yellow. Dorsal pubescence short, entirely decumbent, yellowish white. Surface of head smooth, polished, finely punctured, punctures separated by a diameter or less. Front of head convex between eyes (Fig. 1), eye feebly elongate, narrowed toward base of head. Clypeal apex truncate. Pronotum convex in lateral $1 / 4$, lateral bead


Fig. 7. Female genital plates.
narrow, not reflexed. Pronotal surface slightly alutaceous, shiny, punctures slightly finer than on head, dense, separated by about a diameter in median $1 / 2$, separated by less than a diameter in lateral $1 / 4$. Surface of elytron slightly alutaceous, with intermixed fine, coarse punctures, coarse punctures much larger than pronotal punctures, separated by less than to 3 times a diameter. Intercoxal process of mesosternum with coarse, dense, contiguous punctures. Metasternum smooth, polished, with fine, widely scattered punctures except punctures denser on either side of midline. First abdominal sternum medially smooth, polished, with coarse punctures separated by 3 or 4 times a diameter, lateral $1 / 4$ including postcoxal arc alutaceous, dull, impunctate; postcoxal line on 1 st abdominal sternum extended $2 / 3$ distance to hind margin of sternum; sterna 2-4 with dense, fine punctures in median $4 / 5$ to $7 / 8$ separated by less than to twice a diameter, lateral $1 / 5$ to $1 / 8$ densely alutaceous, impunctate; sterna 5,6 densely alutaceous with fine punctures throughout separated by a diameter or less. Fifth abdominal sternum with posterior margin slightly produced medially; posterior margin of 6th sternum and tergum evenly arcuate. Genitalia with 10th tergum apically truncate; genital plate somewhat rectangular with inner angles rounded, without stylus (Fig. 7).

Type material: Holotype female; Mexico, Sinaloa, 5 mi. W. El Palmito, VII.19.64, H. F. Howden (CNC). Paratype female; 1, Mexico, Sinaloa, 15 mi . W. El Palmito, VII.17.64, H. F. Howden (USNM).

Comments: In addition to the key characters, the two previously described species differ from $E$. howdeni as follows: front of head flat between eyes; eye more slender, elongate; lateral $1 / 4$ of pronotum flat; elytral punctures of uniform size; and sparsely punctured mesosternum. The clypeal apex is truncate in all species except $E$. peregrinus; both $E$. peregrinus and $E$. howdeni lack transverse rugae on sterna 2-4, but
the former has scattered punctures medially and the latter has dense fine punctures throughout. The female genital plate is differently shaped in each species; transverse with strongly rounded apex in E. peregrinus, somewhat elongate with feebly rounded apex in the remaining two species with $E$. weise $i$ having the plate base narrow, lateral margin strongly angled from base to apex, E. howdeni with plate base broad, lateral margin not angled from base to apex. The species is named for Henry Howden, the collector and noted authority on Scarabaeidae.

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## NOTES AND COMMENTS

## THE REDISCOVERY OF THE CLEARWING CHESTNUT MOTH, SYNANTHEDON CASTANEAE (BUSCK) (LEPIDOPTERA: SESIIDAE) IN CONNECTICUT

Bark-boring larvae of clearwing moths cause extensive damage to American chestnut trees (Anagnostakis and Welch, unpubl.), which are surviving chestnut-blightfungus infection because of biological control by hypovirulence viruses (Anagnostakis, 1990; Anagnostakis and Hillman, 1992). Snow and Eichlin (1986) reported this chestnut pest in the southeastern U.S. The insect is illustrated in Eichlin and Duckworth (1988).

## STUDY SITES AND METHODS

Traps were baited with 1 mg of (E,Z)-3-13-octadecadienyl alcohol dispensed from a rubber septum (Snow and Eichlin, 1986). Two lures were used with water-pan traps to collect specimens for preservation. Ten lures were used with Pherocon 1C sticky traps which were placed at six locations in Connecticut where large American chestnut trees (Castanea dentata (Marsh.) Borkh.) were present. One of the locations (Sleeping Giant Chestnut Plantation in Hamden, CT) has trees of all seven species of Castanea and hybrids of most combinations. Other locations were orchard plantings at The Experiment Station Farm in Hamden, CT, and American chestnut trees in mixed hardwood forests in Hampton, CT (open and understory trees), Pomfret, CT (open trees), Rocky Hill, CT (canopy trees), and Roxbury, CT (edge of a landscaped yard).

Traps were set weekly from the end of May, 1989 to the end of June, 1989 and collected and examined when they had been exposed for one week.

## RESULTS

Adult male Synanthedon castaneae (Busck) (a total of 97) were trapped at all of the sites except the forest in Rocky Hill, CT where a single trap was deployed. The largest numbers were found in Hamden, CT in the Chestnut Plantation where 29 were trapped on a sticky trap and two were trapped in a water-pan trap from 1-5 June; from 5-12 June there were 15 on the sticky trap and two in the water trap, and between 12 and 26 June 14 were caught on the sticky trap.

This insect may pose a threat to our chestnut breeding program, and future research will examine the effectiveness of using pheromone traps for control.-Sandra L. Anagnostakis, Kenneth M. Welch, J. Wendell Snow, Kathy Scarborough, and Thomas D. Eichlin, The Connecticut Agricultural Experiment Station, New Haven, Connecticut; Southeastern Fruit and Nut Tree Research Lab, USDA/ARS, Byron, GA; and Division of Plant Industry, California Department of Food and Agriculture, Sacramento, California.

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## ON THE NATURAL HISTORY OF CANOPIDAE (HETEROPTERA: PENTATOMOIDEA)

In moist regions of the Neotropics, the undersides of fallen trees are frequently coated with a layer of fungi which may be inhabited by a diverse assemblage of arthropods. While studying mycophagous Coleoptera in Costa Rica, Bolivia and Peru, I became acquainted with this unusual fauna which includes many heteropterous insects; some mycovores (e.g., Aradidae), other predators (e.g., Reduviidae). Among the familiar residents were some slow moving, shiny black, hemispherical pentatomoids. A few specimens collected from several locations were determined to be species of Canopidae, an infrequently collected family whose biology is unknown.

The Canopidae include eight Neotropical species, with some additional names based solely on immatures (Slater, 1982), all belonging to the genus Canopus Fabricius (McAtee and Malloch, 1928). The monogeneric family has affinities with Scutelleridae and could also be closely related to Megarididae (McDonald, 1979).

Canopidae were frequently encountered during these field trips; however, they were only collected a few times as part of general faunal samples. Although a wide variety of fungal taxa and life stages are typically available, Canopidae are usually found on sporophores of certain fungi (especially thin encrusting polypores) and are often present as both adults and immatures, suggesting that the association with fungi is not incidental. The following are data for 49 specimens representing two species of Canopidae (deposited in the Cornell University Insect Collection) collected by myself
and colleagues (Z. H. Falin, Q. D. Wheeler) who also study mycophagous insects in the Neotropics:

## Canopus burmeisteri McAtee \& Malloch

BOLIVIA: Dpto. La Paz, San Lorenzo (12 km Caranavi), 1-2.I.91, on small brown shelf polypore on undersides of log, ex. Polyporus phillipinensis Berk., JVMlot\#B9116 (3 nymphs); on dark encrusting polypore on undersides of log, ex. Antrodiella sp., JVMlot\#B91-36 (1 \&), JVMlot\#B91-42 (2 nymphs); on undersides of fungus-covered log, ex. Earliella scabrosa (Pers.) Gilbn. \& Ryv., JVMlot\#B91-46 (1 \&, 2 nymphs). PERU: Dpto. Madre de Dios, Río Tambopata Res., 12.I.87, on large flat white polypore, JVMlot\#87-177 (1 nymph); 13.I.87, on flat white polypore, JVMlot\#87-
 on polypore sheet fungus under log, QDWlot\#87-061 (1 nymph); 12.I.87, on $\log$ at night, JVMlot\#87-125 (1 nymph); 12.I.87, on polypore, JVMlot\#87-089 (1 nymph); 16.I.87, ex. polypore on $\log$ in slash-burn area ( 1 nymph ); Dpto. Amazonas, Río Marañón, 1 km downstream from Pongo de Requema, in stream gorge, 26.XII.90, on reddish brown encrusting polypore on underside of log, ex. Porogramme lateritia (Pat.) Pat., JVMlot\#P90-33 (4 nymphs); on brown encrusting polypore on underside of log, JVMlot\#P90-36 (1 ठ).

## Canopus fabricii McAtee \& Malloch

COSTA RICA: Prov. Puntarenas, Las Alturas Bio. Station, Finca Las Alturas, nr. Cotón, 1,540 m, 17.V.92, on undersides of log, JVMlot\#CR92-029 (1 ô); 4.VI.92, on gray encrusting polypore on undersides of log, JVMlot\#CR92-140 (3 ôô, 2 ị, 3 nymphs); Corcovado N. P., Sirena Station, Pavo Trail, elev. 5 m, 3.VI.92, on sheet fungi on downed logs ( 9 nymphs); on shelf fungus on downed logs ( 1 nymph); Ollas
 on sheet fungus at night (2 2 ) ).

Canopids were not the focus of interest during these field trips and, unfortunately, their feeding behavior was never observed. In an attempt to indirectly determine the feeding habits, gut content slides were prepared from three Costa Rican specimens. Considering that the known biology for pentatomoids includes only predation and phytophagy (sap-feeding on angiosperms) (Slater, 1982), it was surprising to find that each gut contained many fungal spores. The spores were of the same type that might be expected from the basidiocarp (a polypore) on which the bugs were observed.

The nature of the association between Canopidae and fungi-encrusted logs is not clear because the immediate source of the spores found in the digestive systems is unknown. Polypore spores have thick walls and may persist intact for some time in the gut of insects. It seems likely that members of Canopidae are obligately or facultatively mycophagous and ingest fungal material directly.-Joseph V. McHugh, Department of Entomology, Cornell University, Ithaca, New York 14853-0999.

## ACKNOWLEDGMENTS

Fungal spores in gut content squashes were determined by R. P. Korf (Cornell University). Fungal sporophore voucher specimens were determined by L. Ryvarden (University of Oslo).


#### Abstract

P. R. Fraissinet, E. R. Hoebeke (Cornell) and R. T. Schuh (American Museum of Natural History) reviewed an early draft of this note. E. R. Hoebeke also made species determinations of Canopidae. Z. H. Falin and Q. D. Wheeler (Cornell) loaned canopids that they had collected. Q. D. Wheeler provided the opportunity to work in Peru in 1987. The research was also funded by Cornell University Graduate School travel grants, Grace Griswold Fund grants, a Hal Moore Competition award, and by NSF Grant No. BSR-87-17401 and Hatch Project No. NY(C)139426 (both to Q. D. Wheeler).


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## MYCOPHAGOUS MIRIDAE? ASSOCIATIONS OF CYLAPINAE (HETEROPTERA) WITH PYRENOMYCETE FUNGI (EUASCOMYCETES: XYLARIACEAE)

Mycophagy in the mirid subfamily Cylapinae has been inferred, but never demonstrated. Cylapus tenuicornis (Say), a North American species of this predominantly tropical group, is widely distributed yet seldom collected. It has been reported from the bark of dead trees and from fungi covering dead wood (Heidemann, 1891; Uhler, 1891; Banks, 1893; Knight and McAtee, 1929). On the other hand, Leston (1961) and Schuh (1974), among others, have suggested that cylapines are predators.

There is little doubt that most Cylapinae live under bark, on rotten logs in association with fungi, and that at least some species frequent pyrenomycete fungi. Schuh (1976) reported observing larger numbers of cylapines under bark than would be expected of a predatory species, while Kelton (1985) reported nymphs and adults of Fulvius imbecilis (Say) from a nearly dry pile of poplar logs in Manitoba "feeding on dipterous and small coleopterous larvae and on the other soft-bodied arthropods found in damp areas under the bark or in fungi." And Herring (1976) discussed associations with the polypore fungi Polyporus caperatus and Coriolopsis corcata inhabited by ciid beetles, whose larvae he supposed them to feed upon. A more complete review of the evidence for predation among cylapines will be given elsewhere (A.G.W., Jr., in prep.).

Predatory habits might be inferred from several lines of circumstantial evidence that are, even in combination, inconclusive. The extraordinary speed and agility of
cylapines could be taken as the mark of a predator, except many potential prey items (such as other fungus-feeding insects) are often sedentary. Many insects, including certain Lepidoptera (Rawlins, 1984) and members of 28 families of Coleoptera ("MYCOL" data base, Cornell University, unpubl. data), are associated with pyrenomycete fungi, suggesting a broad array of potential prey species. In the laboratory, adults and nymphs of Cylapus tenuicornis probed selectively into crevices of fungus-covered wood; the bugs' stylets usually penetrated the fungus and probed bark crevices beneath (A. G. Wheeler and T. Henry, pers. obs.). Finally, the fact that mycophagy has not been observed in phylogenetically related mirids makes the possibility of mycophagy surprising.

Schuh (1976), reconsidering his earlier opinion, stated that existing evidence leans toward mycophagy in cylapines. In support of his hypothesis Schuh cited China and Carvalho (1951), who reported a species of Xenocylapus from a fallen log in South America, and Carvalho (1954), who reported two species of Cylapocoris spp. from an Auricularia fungus "growing on rotten trees in the forest. Since nymphs were taken it is probable that the species feed and complete their life cycle on this fungus" (Carvalho, 1954). Further, Schuh (1976) observed South American Cylapus spp., Valdasus sp., and Xenocylapus sp. from pyrenomycete-covered logs, and collected Cylapocoris sp. from "soft mushroom-like fungi on rotting logs" in Perú. Carvalho and Lorenzato (1978), in reviewing the Cylapinae of Papua New Guinea, observed that "many species feed on fungi."

In the course of collecting insects associated with fungi in Perú and the United States, individuals of two species of Cylapinae were collected from pyrenomycetes, dissected, and observed to have present in their guts ingested materials from host fungi. Thus, the first direct evidence for fungus feeding, in at least one temperate and one tropical species of cylapine, is reported below.

Some common pyrenomycete fungi produce darkly colored, hard and crusty fruiting bodies on decaying wood that can make sections of logs appear from a distance to be burnt. Cylapines may be found resting or running rapidly on the surface of such fungi. They are not infrequently observed, but we have collected relatively few cylapines. This is due in part to the remarkable speed and agility of both immature and mature forms, which makes their capture by hand challenging. Records below are for the two series from which specimens were dissected and found to have fungus material in their guts. Two museum specimens of Cylapus tenuicornis were dissected that did not contain any identifiable inclusions, fungal or otherwise. Specimens of two lots of North American Fulvius spp. also were dissected and found to contain no recognizable fungus parts.

## Cylapus tenuicornis

UNITED STATES: New York, Tompkins County, Trumansburg, Henry Smith Woods, September 4, 1992 (Katherine A. Wheeler and Q. D. Wheeler collectors), Cornell University Insect Collection. One slide-mounted gut was found packed with large numbers of black ascospores. These spores, along with a voucher host specimen, were determined by Drs. Amy Rossman and Gary Samuels to be Hypoxylon fragiforme (Pers.: Fr.) Kickx., a common temperate zone species of the Xylariaceae, Euascomycetes, a pyrenomycete. A second dissection revealed a significant, but less densely packed, volume of identical spores.

## Cylapus sp.

PERÚ: Madre de Dios, Rio Tambopata Reserve, ex Pyrenomycetes, Q. Wheeler 87077, 11 Jan. 1987, J. V. McHugh and Q. D. Wheeler collectors, Cornell University Insect Collection and American Museum of Natural History. Although no xylariaceous spores were present in the gut of this South American Cylapus, there were large numbers of ovoidal structures about 5 microns long that could be conidial stages of a Xylariaceae (Dr. Gary Samuels, pers. comm.). A few hyphal fragments were present as well.

The presence of pyrenomycete spores, conidia, and hyphal fragments in the guts of two cylapine species from North and South America implies a widespread, perhaps ancestral, association of these mirids with fungi. It is conceivable that spores could be ingested in the course of feeding upon mycophagous insects. Given the dense spores in the gut of one specimen, however, this seems unlikely. Neither direct observation of feeding nor breeding of either species was made. Nonetheless, consistent presence of cylapines on pyrenomycete hosts combined with our gut-content analyses provide the most compelling evidence to date that these Miridae may in fact be mycophagous.-Quentin D. Wheeler and A. G. Wheeler, Jr., Department of Entomology, Cornell University, Ithaca, New York 14853-0999 and Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg, Pennsylvania 171109408.

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## THE TAXONOMIC STATUS OF CNEMODUS INFLATUS VAN DUZEE (HEMIPTERA: LYGAEIDAE)

This paper originated from the discovery by the second author of a series of lygaeids obtained by pitfall trapping at several localities in Virginia. Included in this material was a series of 26 specimens of the genus Cnemodus Herrich-Schaeffer, some of which are identifiable as Cnemodus inflatus Van Duzee. It was interesting to note that all of the specimens of "inflatus" were males and all of the mavortius (Say) specimens were females. This gender bias was consistent even though specimens with shortened hemelytra occurred in both sexes.
The status of inflatus has been ambiguous for a long time and it seems desirable here to review the situation and formally synonymize it as a junior synonym of mavortius.
Van Duzee (1915) originally described inflatus from two brachypterous males from North Carolina (Balsam Mountain [W. J. Palmer] and Southern Pines [Manee]) and "four examples received from H. G. Barber." These latter specimens are not referred to by either sex or locality. Van Duzee stated that inflatus was distinguishable by being a "little longer and darker than mavortius, with the rostrum shorter and the anterior lobe of the pronotum more inflated." It should be noted that mavortius varies considerably in color and that Van Duzee's actual description does not indicate a longer labium but rather that it does not reach so far posteriorly (a condition we believe to be due to the larger and more inflated anterior pronotal lobe).

Blatchley (1926) expressed reservations about the validity of inflatus as he noted variation in both characters. He treated it as a "variety" of mavortius.

Froeschner (1944) studied a series from Missouri, noted that the inflated pronotum and short labium occurred only in brachypterous specimens and that even in these brachypters there was considerable variation in the degree of development of both
characters. Froeschner concluded that "the variety inflatus of Van Duzee is apparently superfluous." Thus inflatus was synonymized at that time.

Torre Bueno (1946) disagreed and treated inflatus as a valid species. Slater (1964) in the introduction to his catalogue stated that in almost all cases he followed the literature "slavishly" and since Torre Bueno's treatment of inflatus was the most recent he listed inflatus as a valid species (even though he felt specific status was doubtful because he was aware of Sweet's work cited below). This apparently led Ashlock and A. Slater (1988) to follow the same procedure. Unfortunately Sweet's (1964) study of the biology of Cnemodus mavortius appeared the same year as the Slater catalogue and thus was not cited in the latter (although it is cited without comment under mavortius by Ashlock and A. Slater (1988). The Sweet paper is important not only because it is the only careful study of the biology of mavortius but because it seems to definitely support Froeschner's conclusions that there is striking variation in size and pronotal shape in relation to brachyptery. Sweet also was the first to point out that sexual dimorphism was involved, with the males being variable in size and "both mavortius and inflatus types can be distinguished." Unfortunately however Sweet did not formally synonymize inflatus because he had not seen the type.

The Virginia evidence that only a single species is involved is supported by Connecticut material. Eleven male specimens have been examined. Five of these are macropterous and all have a non-inflated anterior pronotal lobe. Of the six brachypterous males four have inflated anterior pronotal lobes and two do not. It is also evident that the increase in size of the pronotum causes the labium to not extend as far posteriorly as in specimens with non-inflated pronota.

Thus we are convinced that the evidence given by Froeschner and Sweet and our own observations all lead to the same conclusion; i.e., that inflatus Van Duzee is based upon males of mavortius with an inflated anterior pronotal lobe and thus is a junior synonym.
This is not an isolated situation in the Lygaeidae. In the related Pseudocnemodus canadensis (Provancher) the same condition is present. We have examined a series of 45 specimens from a variety of localities. Of these 14 ( 5 males, 9 females) are macropterous and all have a relatively slender, non-inflated anterior pronotal lobe. Of the brachypterous specimens 17 are males and 14 females. All of the females have slender pronota. Of the 17 brachypterous males 10 have an inflated anterior pronotal lobe. The situation appears to be identical to that found to occur in Cnemodus mavortius.

In Harrington's (1980) cladogram Pseudocnemodus and Cnemodus are not sister taxa but are closely related. Interestingly Ashlockaria Harrington, which is in the same clade, appears to show a similar condition although our series is too small to establish this.

It is our belief that similar situations will be shown to exist widely in brachypterous myodochine lygaeids.

It is of interest to note that over a century ago Uhler (1876) noted that in Maryland Cnemodus mavortius "varies much in the breadth of its outline."-James A. Slater and Richard L. Hoffman, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269 and Virginia Museum of Natural History, Martinsville, Virginia 24112.

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## BOOK REVIEWS

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Insects of Panama and Mesoamerica: Selected Studies. - Edited by Diomedes Quintero and Annette Aiello. 1992. Oxford University Press, New York, New York. Hardcover, 720 pp., 1268 illustrations. \$195.00.

Biodiversity, traditionally the province of ecologists, entered the popular vernacular in 1992, when then President George Bush refused to sign the Convention on Biological Diversity prepared for the United Nations conference in Rio de Jeneiro. The biodiversity treaty would encourage the conservation of ecosystems thought to harbor endangered and undiscovered species [predominantly insects and other invertebrates]. A "biodiversity community" has coalesced around efforts to identify species rich areas for conservation consideration, and to prospect for species with potential applications in the biotechnology industry. Systematists have participated only sporadically in plans to document the biodiversity of any fauna. This state of affairs may reflect the conflicting theoretical bases of the two disciplines. Biodiversity studies are essentially faunistic in contrast with the phylogenetic model of modern systematics.

Ongoing efforts to involve systematists in their integral role in biodiversity surveys must reflect what is practical. This does not detract from phylogenetic studies. The editors of Insects of Panama and Mesoamerica have approached this important but difficult assignment by inviting systematic specialists to provide introductions to the biology and literature of many of the insect orders. Most of the specialists provide illustrated keys to the families and genera, and checklists of the described species occurring in Panama, Table 1. By limiting the treatment to the generic level, it is possible to obviate many of the constraints of the faunistic approach which conflict with phylogenetic studies. Taxa at generic and higher levels will usually have a broader biogeographic extent than species, and therefore the effects of the artificial limitation of the treatment to a geopolitical area are diluted. Exemplary treatments of the Tettigoniidae (Nickle) and neuropteroid orders (Henry, Penny and Adams) set a very high standard for the systematic portion of the book.

This book was not designed as a biodiversity survey, but it nonetheless provides perhaps the best available measure of our readiness to tackle such a project in a Neotropical area. The bottom line is that for most of the smaller orders of insects and their allies we could get started tomorrow. The book allows one to sort samples of these orders to a level that would allow them to be submitted to specialists for specific determination. To attempt anything more comprehensive would be prohibitively long and expensive, and would be of interest to a relatively small readership. For the major orders [Diptera, Lepidoptera, Hymenoptera, Heteroptera, Homoptera, and Coleoptera] a different approach will be advisable. Individual volumes of this size will probably be necessary for each. At the present time this might be possible for the major orders excepting the Lepidoptera [exclusive of the butterflies which are known as well as birds]. Considering that the Lepidoptera make up the largest biomass of herbivores, the state of its taxonomy is a major embarrassment.

Table 1. Legend: Mor = morphology discussed and illustrated; Bio = discussion of biology and biogeography; Lit = literature review; Fam = illustrated key to family; Gen = illustrated key to genera; Spe = illustrated key to species; Pan = catalog of Panamanian species; Mes = catalog of Mesoamerican species.

| Taxa | Mor | Bio | Lit | Fam | Gen | Spe | Pan | Mes |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Collembola | Y | Y | Y | Y |  |  | Y | Y |
| Ephemeroptera |  | Y | Y |  | Y |  | Y | Y |
| Odonata |  | Y | Y |  | Y | Y | Y |  |
| Odonata: Gomphidae |  |  |  |  | Y | Y | Y |  |
| Odonata: Zygoptera: Pseudostigmatidae |  | Y | Y |  |  |  |  |  |
| Plecoptera | Y |  |  |  |  | Y | Y |  |
| Embiidina |  |  | Y | Y | Y | Y | Y |  |
| Orthoptera: Tettigoniidae | Y | Y | Y | Y | Y | Y | Y |  |
| Orthoptera: Gryllidae/Gryllotapidae | Y |  | Y | Y | Y |  | Y |  |
| Dermaptera | Y | Y | Y | Y | Y |  | Y |  |
| Isoptera | Y | Y | Y | Y | Y |  | Y |  |
| Isoptera: Termitidae: Apicotermitinae | Y |  | Y |  | Y |  | Y |  |
| Zoraptera | Y | Y | Y |  |  | Y | Y | Y |
| Psocoptera: Psocidae: Thyrsophorinae | Y | Y | Y |  | Y | Y | Y |  |
| Homoptera: Psylloidea (larva) | Y |  | Y | Y | Y | Y | Y |  |
| Heteroptera: <br> Gelastocoridae/Gerridae/Mesoveliidae/Saldidae/Veliidae (Marine) | Y | Y | Y | Y | Y | Y | Y | Y |
| Thysanoptera |  | Y | Y |  |  |  | Y |  |
| Coleoptera: Pselaphidae: Pselaphinae | Y |  | Y |  | Y | Y | Y |  |
| Coleoptera: Lamellicornia: Passalidae | Y | Y | Y |  |  | Y | Y |  |
| Coleoptera: Chrysomelidae: Cassidinae | Y | Y | Y |  | Y |  | Y |  |
| Strepsiptera |  | Y | Y |  |  |  | Y | Y |
| Neuroptera/Megaloptera | Y | Y | Y | Y | Y |  |  | Y |
| Hymenoptera: Mutillidae |  |  | Y | Y | Y |  | Y |  |
| Hymenoptera: Formicidae: Attini |  |  | Y |  |  | Y | Y |  |
| Hymenoptera: Apidae: Meliponinae |  | Y | Y |  | Y | Y | Y | Y |
| Trichoptera |  |  |  |  |  |  | Y |  |
| Trichoptera: Hydroptilidae: Leucotrichiini |  |  | Y |  |  | Y |  | Y |
| Lepidoptera: Hedylidae |  | Y | Y |  |  | Y | Y |  |
| Lepidoptera: Nymphalidae |  |  | Y |  |  |  | Y |  |
| Lepidoptera: Nymphalidae: Hamadryas |  | Y | Y |  |  | Y | Y |  |
| Mecoptera: Bittacidae | Y | Y | Y |  |  | Y | Y | Y |
| Diptera: Pantophthalmidae | Y | Y | Y |  | Y |  | Y | Y |
| Diptera: Asilidae | Y | Y | Y |  | Y |  |  | Y |
| Diptera: Pipunculidae | Y | Y | Y |  |  | Y |  | Y |

Insects of Panama and Mesoamerica also includes several non-taxonomic studies which emphasize important principles for the entomologist working in the Neotropics. The analysis of the distribution and seasonality of the cicadas (Wolda and Ramos) reveals a between-site diversity which, if general among other orders of insects, indicates the restricted geographical distribution of many species. Seasonality is another factor to consider when attempting to appraise biodiversity in the context of conservation biology.

The marine Heteroptera of the Eastern Tropical Pacific (Polhemus and del Rosario Manzano) are treated as the fauna of a natural biome rather than the artificial limitation of a particular geopolitical division. Similar studies of other biomes or specialized habitats will undoubtedly reveal significant insights into the assembly of tropical communities.

Another contribution requiring special note is the treatment of the leaf-rolling weevils (Coleoptera: Attelabidae) by the late George B. Vogt, who presents a long term field study of the host plant associations of these beetles over much of their North American ranges. In this same vein, Loye discusses the host plant relationships and ecological diversity of treehoppers (Homoptera: Membracidae and Nicomiidae). The study of immature stages and host plant associations is central to an understanding of the relationship and biology of many orders. The data are difficult to collect at best, and almost impossible for the visiting entomologist based outside of the tropics. This is the single most important opportunity presented to investigators working for extended periods in the tropics. This reviewer had anticipated that the pioneering work of Annette Aiello, who has spent many years rearing Lepidoptera in Panama, would be presented here, but it unfortunately was not. Other nonsystematic contributions cover aspects of dry season strategies of two butterflies, and the reproductive behavior of Urania.

Not everything is this volume is at the high level of the studies selected for comment. The biogeographic context in particular is weak. Significant biogeographical principles acting across the Panamanian land bridge are ignored, i.e., the angiosperm flora of Central American lowland rain-forest is identical to or derived from South America, whereas the montane flora of South America is of North American origin (Gentry, 1982).

Perhaps the first book a tropical naturalist should own is Flora of Barro Colorado Island (Croat, 1978), but now I recommend the purchase of Insects of Panama and Mesoamerica by every entomologist contemplating study in the Neotropics. This is a big, expensive book, but it would be a mistake to simply copy the chapter dealing with one's narrow interest and miss the opportunity to appreciate the magnificence of this tropical fauna as a whole. There are useful abstracts in English and Spanish as well as a taxonomic index.-Morton S. Adams, Section of Invertebrate Zoology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213.
J. New York Entomol. Soc. 102(1):122-124, 1994

Caterpillars: Ecological and Evolutionary Constraints on Foraging. - N. E. Stamp and T. M. Casey (eds.). 1993. Chapman and Hall, New York. xiii +587 pp. Hard cover. \$75.00 U.S.

Although butterflies and moths are the most well known and widely appreciated invertebrates, comparatively little attention has been given over to their larvae-the caterpillars-except as unwelcome guests in our gardens, forests, and crops. As a
whole caterpillars are extremely uniform morphologically relative to the immature stages of other insect orders. This is most apparent to the poor soul who must work with aged, alcohol preserved specimens that are devoid of their behavior and cryptic and warning coloration. This situation belies the virtual panoply of behaviors and stratagems that caterpillars employ just to survive in a world "hemolymph green in tooth and claw."

The caterpillar agenda is a simple one: eat and not be eaten. No sex, no distractions ... avoid the enemies: inclement weather, the ever present predators and parasites, the pathogens looming on every leaf, competition from other herbivores, and legions of tiered plant defenses. The impact of these factors on the behavior, ecology, and evolution of caterpillars is the subject of this edited volume.

The book is divided into three parts. Eight chapters make up the first section which the editors identified as Constraints on Foraging Patterns of Caterpillars: "Effects of Temperature on Foraging of Caterpillars" (T. C. Casey), "Nutritional Ecology: The Fundamental Quest for Nutrients" (F. Slansky, Jr.), "Foraging with Finesse: Caterpillar Adaptations for Circumventing Plant Defenses" (David Dussard), "Patterns of Interaction Among Herbivore Species" (H. Damman), "Invertebrate Predators and Caterpillar Foraging" (C. B. Montllor and E. A. Bernays), "Potential Effects of Parasitoids on the Evolution of Caterpillar Foraging Behavior" (R. M. Weseloh), "How Avian Predators Constrain Caterpillar Foraging" (B. Heinrich), and "Why Body Size Matters" (D. Reavey). With but a couple exceptions, I found these chapters thoughtful and exceptionally comprehensive-Slansky had nearly 300 citations in his chapter. The natural history in Heinrich's and Dussard's chapters made for fascinating reading.

The second part of the book, Ecological and Evolutionary Consequences: Caterpillar Life-Styles, includes four chapters: "On the Cryptic Side of Life: Being Unapparent to Enemies and the Consequences for Foraging and Growth of Caterpillars" (N. E. Stamp and R. T. Wilkens), "Aposematic Caterpillars: Life Styles of the Warningly Colored and Unpalatable" (M. D. Bowers), "Sociality in Caterpillars" (T. D. Fitzgerald), and "The Effects of Ant Mutualism on the Foraging and Diet of Lycaenid Caterpillars" (M. Baylis and N. Pierce). All four chapters are strong contributions: interesting, informative, and very readable. The first three chapters, like many of the reviews in the first section, were loaded with citations-gold mines for anyone looking for "ins" to the literature on insect-plant interactions.

The last section of the book contains five chapters grouped under Environmental Variation in Time and Space: "Effects of Food and Predation on Population Dynamics" (E. Haukioja), "Caterpillar Seasonality in a Costa Rican Dry Forest" (D. H. Janzen), "A Temperate Region View of the Interaction of Temperature, Food Quality, and Predators on Caterpillar Foraging" (N. E. Stamp), "Biotic and Abiotic Constraints on Foraging of Arctic Caterpillars" (O. Kukal), and "Lepidopteran Foraging on Plants in Agroecosystems: Constraints and Consequences" (P. Barbosa). This section was a mixed bag, often containing the more speculative and narrowly focused chapters. But only the last was disappointing, there being little that wasn't treated with more rigor elsewhere in the book. Barbosa's use of qualifiers was irritating: 28 on pages 548 and 549 , with as many as three in a single sentence.
Separate taxonomic and subject indices conclude the volume. I noted few editorial
problems, and these all trivial. Reproduction of plates and other printing aspects are quite good. The brash neon yellow hard cover should help you find your bearings even during a power outage.

The adaptationist program is alive and well and still producing frass. Few of the authors considered or even mentioned the importance of historical or phylogenetic influences on caterpillar evolution. Too often comparisons made between species are cross familial, even cross superfamilial or ordinal. Only Baylis and Pierce give phylogenetic considerations any serious mention. Clearly this is one of the most important shortcomings not only of the book, but of the studies in this discipline.

Overall, I found the volume outstanding, and well worth the price. The chapters are so thoroughly referenced and up-to-date that anyone studying herbivory or insectplant interactions will need access to the book. All but Janzen's chapter are meant to be reviews. Nevertheless, many of the authors provide considerable unpublished data and observations. Hats off to the individual(s) who added the comprehensive subject and taxonomic indices. These are invaluable, especially to the occasional user. They make the book an important reference to a far larger audience of behaviorists, ecologists, and systematists. I have already found myself grabbing the volume to find out more about silk use in caterpillars, wasp predation, and notodontids, etc.-all made immediately accessible via the indices.

Laying aside technical aspects, I found most chapters interesting and enjoyable, some fascinating - what caterpillars lack in morphological diversity, they more than make up for in behavioral intricacy and complexity. I intend to bring many of the studies in "Caterpillars" into my classrooms. The authors and editors are to be congratulated for setting the table to which many researchers will now be drawn to carve out research programs of their own.-David L. Wagner, Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, Connecticut 06269.

The World of Nematodes.—David R. Viglierchio. 1991. agAccess, Davis, California. 266 pp. $\$ 24.95$.
Many entomologists' knowledge of nematodes is predominantly based on nematodes that are natural enemies of insects and vertebrate-pathogenic nematodes vectored by insects. A few more entomologists are probably aware of the diversity of plant pathogenic nematodes. This book does an excellent job at piquing further interest in this fascinating, ubiquitous, and abundant, yet little-known phylum. The author begins with some statistics that should intrigue and startle many entomologists: the exact number of nematode species is unknown but has been estimated as equal to the number of insect species. Yet, entomologists publish almost 9 times more manuscripts than nematologists, largely because there are few nematologists to study this speciose group.

Dr. Viglierchio's excitement with this subject permeates the pages. While the 13 chapters follow an expected progression of subjects, i.e., evolution, morphology and physiology, ecology, control, and human impact, the reader is captivated throughout
by the recurrent themes of ubiquity and diversity. As examples, nematodes can range from microscopic sizes up to $7-8 \mathrm{~m}$ in length (a parasite of sperm whales). Although nematodes are aquatic, they have colonized every habitat imaginable including hot springs and glaciers, ocean trenches and the top of the Himalayas, as well as many plants and animals. Nematode life strategies are equally varied but the most poorly understood group appears to be the omnipresent microbivorous nematodes; little is known regarding the ecological interactions of this group or even their levels of abundance although it is generally agreed that they must make significant contributions. Examples of nematodes pathogenic to vertebrates are especially compelling because they touch close to home, i.e., eating raw fish as sushi or sashimi can lead to nematode infections, it was proposed to replace all of the sand on Ipanema and Copacabana beaches in Rio de Jeneiro to eliminate pinworm populations, dog heartworm (vectored by mosquitoes) has only recently invaded California but is unfortunately now established in the native coyote populations.

This book does not specifically emphasize insect/nematode interactions although these relationships are discussed. As an entomologist, I found ample opportunity for marveling at the overall similarities and differences between insects and nematodes. The ground plan for nematode morphology is quite standard while insect morphology is much more varied. Yet, the basic structure of nematode cuticle can be very similar to that of insects. Experiments have proven that nematodes use unknown sex pheromones for communication. While insects also use sex pheromones, many of these have been chemically characterized and are even used for control. Plant damage caused by nematodes is frequently less apparent than insect-caused damage. However, similar problems with pesticide resistance plague control of both nematodes and insects although fewer nematicides are available for control of this group.

This book was written as an introductory overview to stimulate the interest of non-nematologists interested in nature. It is clear that attention was paid to defining technical terms within the text and an extensive glossary is also provided to make this book accessible to non-biologists. References are not cited in the text and instead a list of suggested readings is provided toward the end. The many figures, including the traditional color plates showing nematode diseases of plants and animals, are invaluable in helping the reader to visualize descriptions. Abundant examples and statistics keep the text entertaining and down to earth and are accompanied by occasional cartoons and quotes. This book provides a vast amount of information on this phylum but Dr. Viglierchio also shares many of his own views, interpretations, and insights with the reader. For example, Dr. Viglierchio clearly includes his own cynicism regarding the potential use of many strategies for nematode control and mentions his frustration with the limited adoption of nematodes for biological control of insects.

The extremely reasonable price of this soft-cover book is a surprise and delight. Dr. Viglierchio's book is priced to make this information accessible to the general public, and thereby increase knowledge about nematodes. This book has certainly convinced me that nematodes are a significant and fascinating phylum, and I'm sure that many readers will also be persuaded by Dr. Viglierchio that "Nemas are for-ever."-Ann. E. Hajek, Boyce Thompson Institute, Tower Road, Ithaca, New York 14853-1801.

## INSTRUCTIONS TO AUTHORS

The Journal of the New York Entomological Society publishes original research resulting from the study of insects and related taxa. Research that contributes information on taxonomy, classification, phylogeny, biogeography, behavior, natural history, or related fields will be considered for publication. 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.
Manuscripts should be submitted in triplicate to: Dr. James M. Carpenter, Editor, Journal of the New York Entomological Society, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. Contributions must be written in English, double-spaced (including references, tables, captions, etc.) and prepared in the format of a recent issue of the Journal. Manuscripts of any length will be considered for publication. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

Longer manuscripts intended for submission as articles should be accompanied by a brief abstract. Footnotes should be avoided. Tables should be prepared as separate pages; they should be kept to a minimum because of the high cost of typesetting, but may be submitted as photographically reproducible material (see below). The list of references is headed "Literature Cited" and should follow the format indicated in the CBE Style Manual or as found in a recent issue of the Journal. Manuscripts should be printed in roman, bold roman, or underlined roman or bold roman to conform to journal typesetting style. Manuscripts should not contain any italic fonts. Manuscripts containing cladistic analyses should be accompanied by a copy of the data matrix on diskette for verification of the calculations.

Illustrations (originals whenever possible) should be submitted flat, never rolled or folded, with the manuscript. Size of illustrations should be kept manageable and suitable for shipment through the US mail without being damaged. Proportions of illustrations should conform to single column format, actual page size $11.5 \times 17.5 \mathrm{~cm}$. Please assemble illustrations in a compact fashion in order to use journal space effectively. Mount line drawings and halftones on separate plates. Figures should be numbered consecutively. Figure captions should be doublespaced, grouped together and placed at the end of the manuscript. If tables are submitted for photographic reproduction, they should be neat and clean and conform to journal format proportions.

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Authors will receive a reprint order blank with the proofs. Reprints are ordered directly from the printer with no benefit accruing to the Society.

## Journal of the New York Entomological Society

## CONTENTS

Identification of New World Agonum, review of the Mexican fauna, and descrip- tion of Incagonum, new genus, from South America (Coleoptera: Carabidae: Platynini) James K. Liebherr ..... 1-55
On the spider genus Meleon Wanless (Araneae: Salticidae) D. P. Wijesinghe ..... 56-61
Synopsis of the Saicinae (Heteroptera: Reduviidae) of America North of Mexico, with the description of a new species of Saica from the eastern United States R. L. Blinn ..... 62-66
Oligembia vetusta, a new fossil teratembiid (Embioptera) from Dominican amber Claudia A. Szumik ..... 67-73
A new species of Aphelocheirus from Sumatra, and addenda to the world checklist (Heteroptera: Naucoridae) Dan A. Polhemus ..... 74-78
Plusiotis citlaltepetlamayatli, a new species of the lecontei group from Mexico (Coleoptera: Melolonthidae; Rutelinae)
Julian Blackaller-Bages and Leonardo Delgado ..... 79-85
Two new flat bug species from North America (Heteroptera: Aradidae)
T. Väsárhelyi ..... 86-90
Taxonomy and distribution of the Holarctic diving beetle Laccophilus biguttatus Kirby (Coleoptera: Dytiscidae) R. E. Roughley and A. N. Nilsson ..... 91-101
Aradus pericarti, a new species from South America (Heteroptera, Aradidae)
Ernst Heiss ..... 102-106
The first record of Eremochilini (Coleoptera: Coccinellidae: Epilachninae) from Mexico Robert D. Gordon and Natalia Vandenberg ..... 107-110
Notes and Comments
The rediscovery of the Clearwing Chestnut Moth, Synanthedon castaneae (Busck) (Lepidoptera: Sesiidae) in Connecticut Sandra L. Anagnostakis, Kenneth M. Welch, J. Wendell Snow, Kathy Scarborough and Thomas D. Eichlin ..... 111-112
On the natural history of Canopidae (Heteroptera: Pentatomoidea)
Joseph V. McHugh ..... 112-114
Mycophagous Miridae? Associations of Cylapinae (Heteroptera) with Pyreno- mycete Fungi (Euascomycetes: Xylariaceae)
Quentin D. Wheeler and A. G. Wheeler, Jr. ..... 114-117
The taxonomic status of Cnemodus inflatus Van Duzee (Hemiptera: Lygaeidae) James A. Slater and Richard L. Hoffman ..... 117-119
Book Reviews
Insects of Panama and Mesoamerica: Selected Studies Morton S. Adams ..... 120-122
Caterpillars: Ecological and Evolutionary Constraints on ForagingDavid L. Wagner122-124The World of NematodesAnn E. Hajek124-125

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Meetings of the Society are held on the third Tuesday of each month (except June through September) at 7 p.m. in the American Museum of Natural History, Central Park West at 79th Street, New York, New York.

Mailed October 18, 1994

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# RECOGNITION OF THE WEST ASIAN ANCHOMENUS KURNAKOVI AND A. PUNCTIBASIS (COLEOPTERA: CARABIDAE: PLATYNINI) AND MIOCENE EVOLUTION OF THE MEDITERRANEAN AND PARATETHYS SEAS 

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#### Abstract

The two Palaearctic species, Agonum kurnakovi Kryzhanovskij and Agonum punctibasis Reitter, are newly combined as members of the genus Anchomenus Bonelli. Descriptions, distributional data, and means to identify the species are presented. The species are included in a cladistic analysis with the other members of the Anchomenus clade; Tetraleucus picticornis Newman, 10 other species of Anchomenus, the 7 species of Sericoda Kirby, and the 11 species of Elliptoleus Bates. This analysis preserves relationships presented in Liebherr (1991) within and among the other three genera, but defines a new set of cladistic relationships within Old World Anchomenus. These relationships are used to define an area cladogram for the circum-Mediterranean region that is concordant with those of a variety of groups summarized by Oosterbroek and Arntzen (1992). Diversification of Palaearctic Anchomenus is explained in the context of geological evolution of the Mediterranean Sea during the Miocene.


The genus Anchomenus Bonelli is distributed across the Palaearctic Region, and in Vancouveran North America from Alaska to Baja California Sur (Liebherr, 1991). In that revision, I recognized six Old World species and four from the New World. Member taxa possess a characteristic female spermatheca, in which there is a basal reservoir and an apical filament, with the spermathecal gland duct entering the basal reservoir (e.g., Fig. 14). Externally, Anchomenus species exhibit a cordate pronotum (e.g., Figs. 9, 10), often with rugose laterobasal depressions; 1-6 anteroventral and 3-10 posteroventral setae on the profemur. Possession of the latter states of leg setation are synapomorphies at the generic level that distinguish Anchomenus from its sister group (=adelphotaxon of Ax, 1987) composed of the genera Sericoda + Elliptoleus; those genera sharing the synapomorphy of setose parameral apices in the male genitalia (Liebherr, 1991, fig, 292).

While conducting a survey of the over 130 species assignable to the Holarctically distributed genus Agonum Bonelli, I discovered that the West Asian species, Agonum punctibasis Reitter, exhibited a female spermatheca of the Anchomenus type. The configuration of leg setae also differed from that of Agonum species, which generally possess fewer femoral setae than Anchomenus. A thorough comparison of the characters exhibited by $A$. punctibasis convinced me that the species should be transferred to Anchomenus. At the same time, through the courtesy of Dr. O. L. Kryzhanovskij, I had the opportunity to borrow the paratype of Agonum (?Anchodemus) kurnakovi Kryzhanovskij. This single specimen available to me is a male. But, nonetheless, the characters of leg setation, pronotal shape and laterobasal depression rugosity, and
male aedeagal configuration, convince me that this taxon should also be transferred to Anchomenus. This contribution formally combines these two species names with Anchomenus, and provides modifications to my key (Liebherr, 1991) to permit identification of them as members of the genus. I also examine how recognizing these taxa as members of Anchomenus requires reinterpretation of the area relationships defined in a cladistic biogeographic analysis for the genus. The new area cladogram based on the eight Palaearctic Anchomenus is concordant with those summarized by Oosterbroek and Arntzen (1992) for a variety of circum-Mediterranean taxa. Speciation events in the Palaearctic Anchomenus can be accounted for by the successive vicariance and fusion of European and West Asian areas bordering the northern shores of the Mediterranean and Paratethys Seas during the Miocene.

## MATERIALS AND METHODS

Taxonomic, cladistic, and biogeographic methods are those of Liebherr (1991). I have examined additional taxonomic material from the following institutions through the courtesy of their curators: Academy of Sciences, St. Petersburg, Russia (ASSP), O. L. Kryzhanovskij; B. P. Bishop Museum, Honolulu (BPBM), G. A. Samuelson; Hungarian Natural History Museum, Budapest (MNHB), G. Szél; Museum National d'Histoire Naturelle, Paris (MNHP), T. Deuve; Zoologische Staatssammlung, Munich (ZSSM), M. Baehr; and Dremm-Mab Morvan personal collection, Bretagne (DMMC).

## CLADISTIC ANALYSIS

The two additional species were coded for the same characters included in the cladistic analysis of Liebherr (1991), with no new shared-derived characters-i.e., potential synapomorphies-found. A. kurnakovi possesses the derived states for the following characters (states described in Liebherr, 1991, pp. 116-118; state 1 unless noted in parentheses): $5,14,23,24(2), 27,28,32,39,40,50$. A. punctibasis exhibits the derived states for the following: $5,14,20,25(2), 27(2), 28,29,30,32(2), 50,54$. I was not able to examine the female holotype of $A$. kurnakovi, and thus could not score the characters of the female reproductive tract (41-46). Scoring these characters as unknowns (? in HENNIG86, Farris, 1988) results in identical relationships within Anchomenus as presented below, but changes optimizations lower on the cladogram. This causes the rendering of Sericoda into a paraphyletic group, with the Holarctic S. quadripunctata DeGeer and the Himalayan S. lissoptera Chaudoir as secondary and primary outgroups to the Mexican Elliptoleus (see Liebherr, 1991, fig. 292). Accepting this solution amounts to basing classificatory changes in one clade strictly on lack of information in its adelphotaxon. Moreover, in this case, acceptance discounts metacoxal setation as the basis for monophyly of Sericoda (Liebherr, 1991, fig. 292, character 26), even though this character is relatively nonhomoplasious across the Anchomenus clade. Instead, as placement of A. kurnakovi within Anchomenus is supported on other characters-leg setation, pronotal shape, and male aedeagal configuration-and because other Anchomenus species exhibit the plesiomorphic state for all female characters, those plesiomorphic states were assumed for A. kurnakovi.


Figs. 1, 2. Taxon cladograms for Palaearctic species of Anchomenus. 1. Cladistic relationships of 8 currently recognized species. Character-state advances shown by hash marks, reversals by $\times$ 's; synapomorphies outside this clade not shown (see Liebherr, 1991, fig. 292); character numbers correspond to Liebherr (1991, pp. 116-118); cladogram node numbers referenced in text. 2. Topology of taxon cladogram including the 6 species recognized in Liebherr (1991).


Fig. 3. Distributions of Palaearctic species of Anchomenus. $=$ A. cyaneus $\boldsymbol{\Delta}=$ S. dohrnii, $\boldsymbol{\nabla}=$ A. dorsalis, $\diamond=$ A. kurnakovi, $\boldsymbol{\nabla}=$ A. leucopus, $\boldsymbol{*}=$ A. punctibasis, $\star=$ A. virescens, $\triangle=A$. yukilikoi.

Cladistic analysis using HENNIG86 (Farris, 1988), starting the analysis using the $\mathrm{m}, \mathrm{m}^{*}, \mathrm{~h}, \mathrm{~h}^{*}$, and tread commands to search for islands of equally parsimonious trees (Maddison, 1991), resulted in the discovery of 4 equally parsimonious trees of step length 172 , consistency index 0.37 , and retention index 0.69 . These were summarized using strict consensus, or the nelsen option. This consensus tree is identical to that of Liebherr (1991, fig. 292), except within the clade of Palaearctic Anchomenus (Fig. 1). Within the Old World species, the inclusion of two additional species results in retention of only the adelphotaxon relationship of $A$. leucopus Bates and $A$. yukihikoi Habu (Fig. 2). Based on the new evidence, it is most parsimonious to propose A. dorsalis Pontoppidan and $A$. virescens Motschulsky as sister species, and the other six species as their adelphotaxon.

## BIOGEOGRAPHIC ANALYSIS

Both A. punctibasis and A. kurnakovi are distributed in West Asia (Fig. 3). A. kurnakovi is known only from the type locality in the Georgian Adzharo-Imeritinsky Mountains. A. punctibasis is more widely distributed, mostly found east of the Caspian Sea in Iran, Tadzhikistan and Turkmenistan, but with one record in Georgia, from Abkhazia.

If we recognize areas of endemism for this analysis based on species distributions, with the smallest distributions defining areas (Fig. 4), we must add one area (area $\mathrm{J}^{\prime}$ )


Fig. 4. Areas of endemism defined by species distributions of Fig. 3 (see text).
to those previously recognized (Liebherr, 1991). In this analysis, area G represents the areas in which the widespread $A$. dorsalis occurs allopatric relative to other Anchomenus. In smaller areas around the periphery of the range of $A$. dorsalis, this species is sympatric with A. dohrnii (area H, in mountainous Anatolia), A. cyaneus (area I, the Pyrenees and Alps), A. virescens (area J, mountainous Transcaspia), and A. kurnakovi (area $\mathbf{J}^{\prime}$, the Caucasus mountains). From East Asia, the range of the geographically restricted A. yukihikoi (area L, Kyushu) is surrounded by the range of its adelphotaxon, A. leucopus (areas $\mathrm{K}+\mathrm{L}$, Japanese archipelago, Formosa, and Manchuria).

The taxon cladogram (Fig. 1) was converted to a taxon-area cladogram (Fig. 5), with the taxon-area cladogram used to define a fundamental area cladogram in which each area was represented once (Fig. 6). In this analysis, Assumption 0 (Page, 1990) as implemented in the COMPONENT program (Page, 1989) was used to derive a single fundamental area cladogram, meaning that species occupying more than one area supported a most recent historical connection among those areas. Analyses were also attempted using conditions of Assumptions 1 and 2, however the program bombed when 1,190 and 1,142 equally parsimonious trees respectively consumed the program's memory.

The fundamental area cladogram derived under Assumption 0 is characterized by a progressive fragmentation of the Palaearctic from west to east. The vast expanse of northwest Europe is first separated from Anatolia, the southerly Alps and Pyrenees, the mountains of West Asia, and East Asia. The Anatolian region is next isolated,


Figs. 5, 6. 5. Taxon-area cladogram summarizing species' cladistic relationships and distributions. 6. Fundamental area cladogram derived from taxon-area cladogram using Assumption 0. North American Anchomenus comprise adelphotaxon to Palaearctic clade, with Oligocene trans-Beringean vicariance consistent with Allen (1983) and Tangelder (1988). Timing of Palaearctic divergence events derived from geological model (Fig. 7) in concert with taxon cladogram (Fig. 1).
then the Pyrenees and Alps. Finally, the easterly areas surrounding the Caspian Sea are vicariated from the distant Japanese archipelago in East Asia. The final pair of vicariance events includes isolation of Kyushu from the rest of Japan, Formosa, and mainland north China, and vicariance of mountain habitats in Georgia versus Transcaspia. This westerly to easterly vicariance sequence within the Mediterranean region was found to be a general pattern for a number of circum-Mediterranean taxa reviewed by Oosterbroek and Arntzen (1992). Taxa summarized in their paper include Nephrotoma and the Tipula (Acutipalpa) maxima group of the Tipulidae, the Rana ribicunda and Rana temporaria groups (Anura: Ranidae), and the subgenera Triturus and Palaeotriton of Triturus (Urodela: Salamandridae). They proposed a scenario whereby the Balkans and Asia Minor were colonized from the main European land mass, either from the west or north, during Oligocene to early Miocene. This event would have occurred when the area to become Anatolia was connected to western Europe along the northern shore of the Mediterranean (Fig. 7A; Steininger and Rögl, 1984). Subsequent connection of Anatolia to Asia Minor, and vicariance between Anatolia and western Europe (Fig. 7B), followed by total isolation of Anatolia (Fig. 7C) permitted emergence of a Balkan fauna. In Mid-Miocene, this fauna spread throughout Europe when land connections were reinstated (Fig. 7D, E). The Caucasus


Fig. 7. Geological history of the Mediterranean region throughout the Miocene (redrawn from Steininger and Rögl, 1984). Land margins stippled; current Black and Caspian Sea margins shown by dotted lines; ages of land configurations shown in millions of years (Ma).
first emerged as a separate mountain range at this time, with isolation first about 14.5 Ma (Fig. 7D), and again in Late Miocene (Fig. 7F).

The fundamental area cladogram for Palaearctic Anchomenus (Fig. 6) is largely concordant with this scenario. The initial vicariance of European and Anatolian lineages (areas G, H, Fig. 6; Fig. 7A, B, C) was followed by dispersal into Europe by the Anatolian lineage when Anatolia was again contiguous with western Europe (Fig. 7D, E). This led to colonization of the Pyrenees and the Alps (Fig. 6, area I; Fig. 7E, F). The Pyrenees were formed by two bouts of orogeny, the first dated Paleocene to Eocene, the second in the Late Miocene, about 10 Ma (Plaziat, 1981; Oosterbroek and Arntzen, 1992). Given initial vicariance within this lineage at 23 Ma , or Early Miocene, only the second bout of Pyrenean orogeny figures in the isolation of populations comprising Anchomenus ancestors.

To the east, occupation of Anatolia could have permitted colonization of areas to the south of the present Caspian Sea as early as 17 Ma (Fig. 7B). Based on the fundamental area cladogram for Anchomenus (Fig. 6), these areas were not colonized until somewhat later, contemporaneous to dispersal westward to the proto-Alps and
proto-Pyrenees (Fig. 7D, E). The Caucasus mountains were first isolated in MidMiocene (Fig. 7D), suggesting the earliest possible time of vicariance for the Caucasus and Transcaspia (areas J and J', Fig. 6) relative to areas to the west (i.e., areas H, I, Fig. 6). If we assume isolation in the Pyrenees at 10 Ma , it is more logical to assume a later isolation of the Caucasus leading to present-day Anchomenus species; i.e., during the second bout of isolation and orogeny about 11 Ma (Fig. 7E). As noted below, this choice reflects discordance between the fundamental area cladogram, and a biogeographic scenario derived directly from the taxon cladogram.

The East Asian areas in China, Formosa, and the Japanese archipelago (areas K, L, Fig. 6) are most closely related to the areas surrounding the Caspian Sea (areas J, $\mathrm{J}^{\prime}$ ). Large tracts of non-forested steppe vegetation already occupied intermediate areas by the Pliocene (Frenzel, 1968), dating vicariance between the Japanese and Caspian areas from 10 to 3 Ma . Whether or not the large intermediate regions are currently inhospitable to Anchomenus remains a goal for future survey and study.

Finally, the two sister area relationships, J and $\mathrm{J}^{\prime}$, and K and L , can be dated as Pliocene to Pleistocene. During the Pleistocene glacial episodes, riparian vegetational belts connected the mountainous regions surrounding the Caspian Sea (Frenzel, 1968), and could have provided means to maintain connections among riparian Anchomenus in the region. These riparian belts were eliminated or moved northward during interglacial periods, affording the means to isolate populations on either side of this sea.

In Japan, the occurrence of $A$. yukihikoi at only the type locality on Kyushu, with its range in the midst of its adelphotaxon, A. leucopus, suggests speciation of the former via isolation of a peripheral population of their common ancestor.

Given the above scenario based on the fundamental area cladogram, and the geological history of the circum-Mediterranean region, the taxon cladogram (Fig. 1) can be reexamined, with tentative dates assigned to the various nodes. The initial vicariance (node 1) would be dated as early Miocene, resulting in the ancestor of $A$. dorsalis $+A$. virescens in northwest Europe, and the ancestor of $A$. dohrnii plus the rest of the species in Anatolia.

Differentiation within Anatolia proceeded by colonization of areas to the east, i.e., the Caucasus, leading to speciation of $A$. kurnakovi (node 3, Fig. 1). Based on the taxon cladogram, this event occurred after Anatolian isolation (Fig. 7C), but before evolution of the Pyrenees (Fig. 7F). However, based on the fundamental area cladogram (Fig. 6), isolation of the Caucasus occurred after development of the presentday Pyrenees and Alps. This tension can be resolved by recognizing that the general summary of all species information using Assumption 0 supports the later Caucasian vicariance, whereas the cladistic position of $A$. kurnakovi supports the earlier vicariance. Because of Assumption 0, the general summary is heavily influenced by the distribution of $A$. punctibasis in areas J and $\mathrm{J}^{\prime}$ (Figs. 1, 3, 5), and the adelphotaxon relationship of $A$. punctibasis versus $A$. leucopus + A. yukihikoi (Figs. 1, 5). As a means of resolution, it is suggested that $A$. kurnakovi was isolated in the Caucasus at Mid-Miocene (Fig. 7D), whereas A. punctibasis first occupied the area in Late Miocene (Fig. 7E).

Range expansion in Mid-Miocene (Fig. 7D, E) during orogeny of the present-day Pyrenees and Alps resulted in colonization of a large area of Europe and Asia, followed by speciation of $A$. cyaneus (node 4, Fig. 1). Isolation of the European mountain
ranges from those east of the Bosporus (Fig. 7F) by Late Miocene formed the basis for the final diversification in Palaearctic Anchomenus. These events include Miocene to Pliocene vicariance of the Caucasian and Transcaspian regions from the coastal forests of China and Japan (Frenzel, 1968), resulting in speciation of A. punctibasis (node 5, Fig. 1).

Two final cladistic events include speciation of the East Asian A. leucopus and $A$. yukihikoi (node 6, Fig. 1), and the West Asian A. virescens and A. dorsalis (node 7, Fig. 1). Both sister-species pairs exhibit a pattern in which the range of the narrowly distributed species is within the range of its more widespread sister (Fig. 3), suggesting that speciation proceeded by isolation of peripheral populations followed by recolonization of the narrowly distributed species' range by the more widespread species, i.e., the centrifugal speciation model (Brown, 1957). Speciation of A. leucopus and A. yukihikoi likely occurred in Pliocene to Pleistocene, that age constrained by the time of origin of $A$. punctibasis (Fig. 1). Speciation of $A$. dorsalis and A. virescens may have occurred in the Pleistocene, Pliocene, or earlier. The timing of this event is not narrowly delimited by more basal cladistic relationships, as these two species form the sister group of the other six Palaearctic species. Separation of mixed conifer/ deciduous forest in Europe versus the Caucasus, as observed at the end of the Pliocene (Frenzel, 1968, fig. 2), would have afforded the type of vegetation pattern likely to be associated with isolation of populations leading to speciation of $A$. virescens. Subsequent vegetational movements during the Pleistocene would have provided the means to reestablish sympatry between $A$. dorsalis and $A$. virescens.

This scenario provides much more specific conditions for diversification of Pa laearctic Anchomenus than I previously proposed (Liebherr, 1991). Adoption of this scenario requires modification of timing for the origin of Anchomenus within the four-genus Anchomenus clade. I previously suggested that the Old World and New World Anchomenus were isolated by climatic cooling across Beringia in Mid- to Late Miocene (starting 12 Ma ). The considerations of Palaearctic Anchomenus presented here suggest that this vicariance was older, perhaps as early as Late Oligocene (2324 Ma ). Such a change would still be consistent with the earliest divergence event in the Anchomenus clade; i.e., the basal divergence of Tetraleucus picticornis Newman, distributed in the eastern United States, from the rest of the group in Late Eocene ( 38 Ma ). That event is still accountable to the most recent opening of the Atlantic Ocean (Noonan, 1986; Tangelder, 1988).

The Oligocene ( $38-25 \mathrm{Ma}$ ) would have seen range expansion of Anchomenus across the Palaearctic and into Vancouveran North America, as the Turgai Straits closed at 30 Ma uniting Asia-America with Europe (Noonan, 1986). The diversification of Old World Anchomenus starting in Early Miocene, as presented here, establishes Late Oligocene vicariance across Beringia between the ancestors of the present-day Old World and New World lineages within the genus. Tangelder (1988) also hypothesized initial Oligocene aged trans-Beringean vicariance within the dorsalis species group of the crane fly genus Nephrotoma (Diptera: Tipulidae), though later Pliocene and Pleistocene trans-Beringean relationships are also in evidence for this group. Allen (1983), reviewing relationships in a number of temperate forest arthropod taxa, found that Oligocene vicariance across Beringia was supported by taxonarea relationships in five of the nine taxa he studied, with the other four taxa uninformative on this issue.

In Liebherr (1991, fig. 378), I hypothesized Miocene vicariance as the agent causing divergence of Elliptoleus and Sericoda, those two genera comprising the adelphotaxon of Anchomenus. The Oligocene date of origin, hypothesized above, for ancestral Anchomenus suggests the time of divergence of Sericoda and Elliptoleus may be earlier than Miocene, constrained only by the origin of ancestral Anchomenus during the Oligocene ( $38-25 \mathrm{Ma}$ ). This suggests that the Mexican Elliptoleus may have started diversifying contemporaneously with the initial Oligocene formation of the Sierra Transvolcanica (Halffter, 1987). Such a conclusion allows taxa exhibiting Halffter's Nearctic Pattern to be as old as Oligocene, and not restricted to Plio-Pleistocene invasion of Mexico as he initially suggested (Halffter, 1976).

## TAXONOMIC TREATMENT

The following couplets should be inserted into the Key to Adults of the Anchomenus Clade (Liebherr, 1991, pp. 26-30), allowing identification of $A$. kurnakovi and $A$. punctibasis. Figures mentioned with a capitalized legend are in this paper, those noted with lowercase are in Liebherr (1991). Parenthetical pages numbers following species names refer to Liebherr (1991).

## ADDITION TO KEY TO ADULTS

| 6(5). | Pronotum very evidently punctate (fig. 124, Fig. 9); elytral striae with closely set, regular, and coarse punctures |
| :---: | :---: |
| $6^{\prime}$. | Pronotal punctures much fainter, aligned in transverse rows (fig. 125); elytral striae with indistinct and irregular punctures ................ Anchomenus yukihikoi (p. 46) |

6a(6). Upper body surface brunneous, legs testaceous; pronotum strongly cordate, laterobasal margins strongly concave, hind angles prominent (Fig. 124)

# 6a'. Upper body surface and legs dark; pronotum with laterobasal margins straight before denticulate hind angles (Fig. 10) <br> Anchomenus punctibasis 

7(5). Profemora with 2-4 posteroventral setae (figs. 56-63) ................................ 8
7'. Profemora with 5-8 posteroventral setae (fig. 55) .................................. 7a
$7 \mathrm{a}(7)$. Mesofemora with 3 anteroventral setae (Fig. 11) ............. Anchomenus kurnakovi
$7 \mathrm{a}^{\prime}$. Mesofemora with 6-10 anteroventral setae (fig. 64) ..... Anchomenus dohrnii (p. 37)

## DESCRIPTIONS

## Anchomenus kurnakovi (Kryzhanovskij), New Combination

Agonum (? Anchodemus) kurnakovi Kryzhanovskij, Kryzhanovskij and Abdurakhmanov, 1983:529.

Diagnosis. Head above, pronotum, and elytra brilliant metallic blue-green; pronotal hind angles setose, thereby diagnosable from A. cyaneus Dejean; metathoracic flight wings reduced to vestigial flaps; metacoxae trisetose, inner seta present.

Description. Dorsal body surface metallic blue with green reflection; femora and ventral body surface piceous; tibiae, tarsi, mouthparts, and antennae slightly paler, brunneous. Eyes small in diameter but convex, ocular ratio 1.45. Pronotum cordate, laterobasal margins sinuate, strongly elevated outside wrinkled laterobasal depressions (Fig. 9); pronotal disc with well-developed impressions each side of midline;


Fig. 8. Anchomenus kurnakovi paratype ô.
anterior transverse impression well-defined, discal area anterad impression depressed. Elytra flattened dorsally, lateral margins laterally explanate (Fig. 8); elytral intervals moderately convex; elytral striae nearly smooth, only faint indications of punctures in basal half. Three dorsal elytral setae and 18 lateral elytral setae. Metepisternum foreshortened, mesal margin $1.15 \times$ length of anterior margin; flight wings reduced to vestigial flaps. Profemur with 2-3 anteroventral setae and 6-8 posteroventral setae. Mesocoxa with 1 ridge seta; mesofemur with 3 anteroventral setae. Metacoxa trisetose, the inner seta present. Metafemur with 3 anteroventral setae. Fourth metatarsomere with inner and outer subapical setae. Fifth metatarsomere with 6 long ventral setae. Male abdomen with 1 apical seta each side.

Head with shallow isodiametric mesh microsculpture. Pronotal disc with transversely stretched isodiametric to transverse mesh microsculpture. Elytra with welldeveloped and slightly transversely stretched isodiametric mesh microsculpture (observed on ô paratype).


Figs. 9, 10. Pronota of Anchomenus. 9. A. kurnakovi. 10. A. punctibasis.

Standardized body length 7.8-8.0 mm (from Kryzhanovskij and Abdurakhmanov, 1983).

Male genitalia. Parameres basally melanistic, apically testaceous. Aedeagal median lobe with bluntly rounded apex (Fig. 12), lobe straighter near middle of length than closer to apex.

Types. Holotype 9 (ASSP): Georgia, Adzharo-Imeritinsky mountains, north slope, upper Supsa R., 21-VI-1958, B. Kurnakov (not seen). Paratype ô (ASSP: incorrectly noted as female in Kryzhanovskij and Abdurakhmanov [1983]) with same data (specimen was examined).

Distributional range. Known only from the types collected in the Georgian mountains (Fig. 3).

Anchomenus punctibasis (Reitter), New Combination

## Agonum punctibasis Reitter, 1894:123.

Diagnosis. Body and legs uniformly piceous; pronotum with denticulate hind angles, convex laterobasal margins, and densely punctate laterobasal depressions and median basal area (Fig. 10); discal elytral striae strongly punctate in basal half; 6-8 anteroventral setae on mesofemur.

Description. Eyes large and convex, ocular ratio 1.80. Pronotum with convex laterobasal margins before the denticulate hind angles (Fig. 10); laterobasal depressions shallow; pronotum densely punctate across base and forward laterally to onehalf of length. Elytral intervals convex; elytral striae strongly and regularly punctate in basal half, especially on disc, weakly punctate in apical half of elytron. Three dorsal elytral setae and 16-17 lateral elytral setae. Metepisternum elongate, flight wings fully developed. Profemur with $8-10$ anteroventral setae and 6 posteroventral


Figs. 11-15. 11. Left mesofemur, Anchomenus kurnakovi, ventral view. 12, 13. Aedeagal median lobe, right side view (ventral side in repose). 12. A. kurnakovi. 13. A. punctibasis. 14, 15. Female reproductive tract structures of $A$. punctibasis. 14. Female reproductive tract, ventral view. 15. Enlarged ventral view of left gonocoxa. bc = bursa copulatrix, $\mathrm{co}=$ common oviduct, $\mathrm{gcI}=$ basal gonocoxite, $\mathrm{gcII}=$ apical gonocoxite, saf $=$ spermathecal apical filament, sbr $=$ spermathecal basal reservoir, $\mathrm{sg}=$ spermathecal gland.
setae. Mesocoxa with 4-5 ridge setae; mesofemur with 7-8 anteroventral setae, 5 setae on dorsal half of anterior surface, plus 15-17 setae in a row along dorsal surface. Metacoxa trisetose, inner seta present; metafemur with 6 anteroventral setae. Fourth metatarsomere with inner and outer subapical setae; fifth metatarsomere with 6 ventral setae subequal to width of tarsomere at points of insertion. Abdomen with 2 setae each side at apex in females, 1 seta each side in males.

Head with well-developed isodiametric mesh microsculpture on neck, vertex shinier with weak microsculpture. Pronotal disc with shallow transverse mesh microsculpture, median base with irregular transverse mesh, laterobasal depressions with more evident, transversely stretched isodiametric sculpticells. Elytral intervals with granulate isodiametric microsculpture.

Standardized body length $8.5-9.3 \mathrm{~mm}$.
Male genitalia. Parameres basally melanistic, apically brunneous. Aedeagal median lobe narrow throughout length, apex tightly rounded (Fig. 13); shaft slightly darker at parameral articulation, testaceous apically.

Female reproductive tract. Penultimate gonocoxite with apical fringe of 12-13 larger setae (Figs. 14, 15), with 1-2 smaller setae slightly basad apical fringe (Fig. 15). Apical gonocoxite with 1-2 lateral ensiform setae, 1 dorsal ensiform seta, and 2 nematiform setae in apical depression. Bursa copulatrix with lumenal microtrichia, densest and longest near entrance of spermatheca and common oviduct (Fig. 14); common oviduct with well-developed lumenal microtrichia. Spermatheca with basal reservoir and apical filament about $3 \times$ length of reservoir. Spermathecal gland duct entering about middle of length of basal reservoir.

Type. Described from more than one specimen from the Sefir-Kuh (now Safid Kuh) mountains north of Herat, Afghanistan, based on Reitter (1894) considering the length of specimens to be $9-10 \mathrm{~mm}$. The types could not be located in the Reitter collection, Hungarian Natural History Museum, Budapest (G. Szél, pers. comm.). I have based the identification on the 2 Hauser specimens (MNHB) from Oasis Tedzhen (Apfelbeck collection, determined by A. Jedlička, confirmed by J. Schmidt, Rostock). Tedzhen is approximately 300 km from the type locality.

Distributional range. Found in Transcaspia, from Turkmenistan and Iran east to Tadzhikistan. Also known from in the Abkhazian region of the Caucasus (Fig. 3).

Material examined. GEORGIA: Abchasien [= Abkhazia] (ZSSM, 2). IRAN: Aliabad, V-1967 (DMMC, 1); Chaldée Persane, Kélateh = [Qalat], 300 m, 1904 (MNHP, 1); Zabol, Berang, V-1950 (DMMC, 1). TADZHIKSTAN: Dushanbe Prov., Nishni Piandsh, VI-1986 (DMMC, 3). TURKMENISTAN: Oasis Tedzhen, VIII-1903 (BPBM, 6; MNHB, 2).

Nomenclatural note: There remains potential confusion concerning the synonymy of Anchomenus punctibasis. Specimens at Budapest of the Tedzhen series collected by Hauser have been considered A. punctibasis Reitter by Jedlička and Schmidt. The Bishop Museum's portion of the series was determined as Anchomenus turkestanicus Ballion (1871) by an unknown determiner. This name is based on specimens from Khodzhent, Tadzhikistan, with the type deposited in Ballion's collection, now at the University of Odessa, Ukraine (O. L. Kryzhanovskij, pers. comm.). This type was unavailable to me, and Ballion's description is inadequate for identification. Therefore, I cannot evaluate this potential synonymy.

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# A NEW GENUS AND FOUR NEW SPECIES OF COLPURINI (HEMIPTERA: HETEROPTERA: COREIDAE) FROM NEW GUINEA 

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#### Abstract

A new genus and four new species from New Guinea are described in the tribe Colpurini (Coreidae). The relationships of the genus are stated to be with Hygia. Dorsal view illustrations, and drawings of the head, pronotum and male and female genitalia are provided.


Recently I have been engaged in a revisionary study of the tribe Colpurini (Coreidae). This tribe has undergone extensive speciation in the Indo-Pacific Islands, contains many undescribed species and will eventually prove to be of considerable importance in zoogeographic studies. This paper is presented at this time to describe a new genus and four new species that occur in New Guinea, so that they may be available for use in a faunal study of the Coreidae of this island. Little is known of the biology of these species and probably the majority of species are adapted to forest edge and forest habitats, and live on or beneath low plants or among decaying plant material; a few of them are pests of field crops (Dolling, 1987; Brailovsky, 1990; Brailovsky et al., 1992).

The following abbreviations are used in the text: Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); Instituto de Biología de la Universidad Nacional Autónoma de México (IBUNAM); Museum of Comparative Zoology, Harvard University (MCZH); Rijksmuseum van Naturlijke Histoire, Leiden, Netherlands (RNHL).

All measurements are in millimeters.

## Lothygia, new genus

Description. Head. Longer than wide, pentagonal and dorsally slightly convex; tylus apically truncate or with a small spiny projection, extending anterior to juga and seen laterally extending above them; juga unarmed and thick; antenniferous tubercles unarmed, with truncate apex or with small lateral lobe-like projection; sides of head in front of eyes unarmed, straight and longer than total length of eye; antennal segment I robust, thickest, curved outwards and shorter than head; segments II and III cylindrical and relatively robust; segment IV fusiform; antennal segment II the longest, segment IV longer than I and I and III almost equal; ocelli conspicuously tuberculate; preocellar pit deep, diagonally excavated; eyes spherical; postocular tubercle protuberant; bucculae rounded, short, not extending beyond antenniferous tubercles, with a sharp spiny middle projection; rostrum reaching anterior third or extending beyond posterior edge of abdominal sternite VII. Thorax. Pronotum. Wider than long, trapeziform, moderately declivent; anterior collar wide; frontal angles produced forward as conical teeth; anterior half of anterolateral edge straight and posterior half convex; humeral angles rounded, not exposed; posterolateral and pos-
terior edge straight; callar region with two short elevations, separated along midline by a longitudinal furrow; posterior margin with a transverse ridge. Anterior lobe of metathoracic scent glands reniform, posterior lobe sharp and shorter. Legs. Fore and middle femora with two rows of small and obtuse spines, running along ventral surface; posterior femora with small, anteapical obtuse spines difficult to see; tibiae cylindrical, sulcate. Scutellum. Triangular, flat, wider than long; apex short, acute. Hemelytra. Macropterous, reaching the posterior margin of the last abdominal segment; apical margin obliquely straight, with a short apical angle reaching almost the middle third of the hemelytral membrane; costal margin emarginated, slightly convex; hemelytral membrane with few bifurcate veins. Abdomen. Connexiva higher than body; posterior angle of connexiva complete, not extending into a short spine; abdominal sternites with medial furrow projecting to anterior edge of sternite V . Integument. Dorsal surface dull and ventrally bright, polished. Ventral head, pronotum, scutellum, clavus, corium, thorax, abdomen and exposed parts of genital segments of both sexes punctate. Body covered by short to long decumbent scattered bristlelike hairs; antennae and legs with few long erect hairs. Male genitalia. Genital capsule. Posteroventral edge laterally produced into short blunt lobes and between them with a large (Fig. 5) or shorter (Fig. 4) median almost straight plate, or well posteroventral edge heart-shape (Fig. 7) or sinuate and laterally poorly exposed (Fig. 6). Parameres. Figures 8-15.

Female genitalia. Abdominal sternite VII with plica and fissure; plica noticeably elevated, apically rounded and leaving only a short fissure uncovered; gonocoxae I enlarged dorso-ventrally, in caudal view opened (Fig. 17) or closed (Fig. 19), in lateral view slightly triangular, with superior half broad and inferior half slender or elongate and apically lobated; outer margin with superior convexity; paratergite VIII short, triangular, with visible spiracle; paratergite IX squarish (Figs. 16-19). Spermatheca. Figure 20.

Type species. Lothygia papuana, new species.
Etymology. Named for Dr. Antonio Lot Helgueras, in recognition of his distinguished services toward the advancement of knowledge of the Mexican aquatic vegetation.

Distribution. New Guinea.
Discussion. This genus is closely related to Hygia Uhler, sharing with it the following characters: juga unarmed, head not elongated, sides of head in front of eyes unarmed, ocelli present, bucculae with sharp middle projection, humeral angles rounded, not exposed and plica and fissure of abdominal sternite VII of the female present, differing primarily by the following combination of characters: body remarkably robust, antennal segments II and III robust, head longer than wide, rostrum reaching anterior third or extending beyond posterior edge of abdominal sternite VII, frontal angles of pronotum slightly produced forward as conical teeth, fore and middle femora armed with two rows of small and obtuse spines, running along ventral surface, scutellum wider than long and pleural margin of abdominal sternites III to VII always bright orange yellow.

In Hygia (Pterocolpura) Blöte antennal segments II and III slender, head wider than long, rostrum reaching posterior margin of abdominal sternite V , frontal angles of pronotum conspicuously expanded like broad wings, femora unarmed, scutellum longer than wide and pleural margin of abdominal sternite III to VII never bright orange yellow.


Figs. 1-7. 1-3. Head and pronotum in dorsal view of Lothygia spp. 1. L. papuana, new species. 2. L. sandaracine, new species. 3. L. enarotadi, new species. 4-7. Caudal view of the male genital capsule of Lothygia spp. 4. L. papuana, new species. 5. L. enarotadi, new species. 6. L. sandaracine, new species. 7. L. cordigera, new species.

In Hygia (Sphinctocolpura) Breddin the head wider than long, scutellum wider than long or almost equal, rostrum shorter, reaching anterior third of abdominal sternite V , frontal angles of pronotum conical, fore and middle femora with only two short anteapical spines, plica of abdominal sternite VII of the female transversely elongated and never surpassing the middle of that segment and the pleural margin of abdominal sternite III to VIII never bright orange yellow.

The only species previously recorded from New Guinea and belonging to the genus Hygia was H. (Eucolpura) lugubris (Walker) (1871). The subgenus H. (Eucolpura) Breddin is clearly distinguished for the genae armed with rectangular and short teeth, antennal segment I longer than 2.70 mm , rostrum reaching middle third of abdominal sternite IV and plica of abdominal sternite VII of female transversely elongated and




Figs. 8-15. Parameres of Lothygia spp. 8, 9. L. papuana, new species. 10, 11. L. cordigera, new species. 12,13 . L. enarotadi, new species. $14,15 . L$ sandaracine, new species.
never surpassing the middle of that segment. In Lothygia, new genus, the genae are unarmed, the antennal segment $I$ is shorter than 2.00 mm , rostrum longest and plica noticeably elevated leaving only a short fissure uncovered.

## Lothygia papuana, new species

Figs. 1, 4, 8, 9, 16, 17, 20, 21, 24
Description. Dorsal coloration. Head black; space between eye-ocelli yellow; antennal segments I to III dark red and IV dark orange with basal third dark red; pronotum dark red orange with anterior third dark black red; scutellum black with apex ochre; clavus and corium orange; hemelytral membrane dark brown with black spots and following areas yellow: basal angle and apical margin; connexival segments bright orange yellow with posterior third black (on some specimens entirely yellow); abdominal segments I-VII dark brown to black. Ventral coloration. Bright dark red with following areas bright orange yellow: anterior lobe of metathoracic scent gland and pleural margin of abdominal sternite III to VII; acetabulae and prothorax bright


Figs. 16-20. 16, 17. Female genital plates of Lothygia papuana, new species. 16. Lateral view. 17. Caudal view. 18, 19. Female genital capsule of Lothygia cordigera, new species. 18. Lateral view. 19. Caudal view. 20. Spermatheca of Lothygia papuana, new species.
dark orange; rostral segments I-II dark red and III-IV paler; legs bright dark red with a complete or incomplete ochre ring located on the basal third of tibiae. Structures. Antenniferous tubercles unarmed, with truncated apex; tylus apically with a small spiny projection; rostrum reaching posterior edge of abdominal sternite VII. Genitalia. Genital capsule. Posteroventral edge laterally produced into short blunt lobes and between them a medium-sized plate (Fig. 4). Parameres. Figures 8, 9.

Measurements. Male. Length head: 2.40; width across eyes: 1.90 ; interocular space: 1.37; interocellar space: 0.90; preocular distance: 1.60 ; length antennal segments: I, 1.60; II, 2.35; III, 1.50; IV, 1.70. Pronotal length: 2.80 ; width across frontal angles: 2.10; width across humeral angles: 4.75. Scutellar length: 2.05 ; width: 2.35. Total body length: 14.05 .

Female. Color. Similar to male. Hemelytral membrane with or without black spots; abdominal and connexival segments VIII and IX black; genital segments bright dark red; paratergite VIII orange yellow or bright dark red. Structures. Rostrum reaching anterior third of abdominal sternite VII; gonocoxae I in caudal view dorso-ventrally opened (Figs. 16, 17). Measurements. Length head: 2.65; width across eyes: 2.05; interocular space: 1.30; interocellar space: 0.75 ; preocular distance: 1.75 ; length antennal segments: I, 1.70; II, 2.60; III, 1.60; IV, 2.10. Pronotal length: 2.75 ; width across frontal angles: 1.85 ; width across humeral angles: 5.15 . Scutellar length: 2.35; width: 2.55 . Total body length: 15.50 .

Holotype male. PAPUA NEW GUINEA: SE: MILNE BAY PROV: Dumai Creek Camp, 25.III.85. F. J. Radovsky. Deposited in BPBM.

Paratypes. NEW GUINEA: Lower Mist Camp (1,350-1,800 mts.), 13-31.I. 39 and I.II.39. L. J. Toxopeus (Neth. Ind. American New Guinea Exp.). Three males, five females. Deposited in RNHL and IBUNAM. NEW GUINEA: Telefomin, III-VI. 71. A. B. Mirza. Three males, three females. Deposited in BPBM and IBUNAM. NEW GUINEA: NW: WISSELMEREN: Enarotadi (1,800-1,900 mts.), 26.VII.62. J. Sedlacek. One male. Deposited in IBUNAM. NEW GUINEA: NE: EAST HIGHLANDS: 20 km SW, Kainantu ( $1,800 \mathrm{mts}$. ), 16.I.66. J. Sedlacek. One male. Deposited in IBUNAM. NEW GUINEA: NE: EAST HIGHLANDS: 10 km , NE of Lufa ( 1,800 2,100 mts.), 21.I.66. J. and M. Sedlacek. One male, three females. Deposited in BPBM and IBUNAM. NEW GUINEA: Mt. Kundip (nr. Hagen) (7,200'), 10.IX.63. T. Schoener. Three females. Deposited in MCZH and IBUNAM. NEW GUINEA: OKAPA: Purona ( $1,800 \mathrm{mts}$.), 17.I.66. J. and M. Sedlacek. One female. Deposited in BPBM. NEW GUINEA: SE: Woitape (1,550-1,750 mts.), 2-3.XI.65. J. and M. Sedlacek. One female. Deposited in BPBM. NEW GUINEA: NE: WAU: Bulldog Rd. (2,100-2,400 mts.), 19.V.67. G. A. Samuelson. One female. Deposited in BPBM. NEW GUINEA: NE: WAU: Bulldog Rd., 40 km S of Wau, 22-31.V.69. J. and M. Sedlacek. One female. Deposited in BPBM.

Etymology: This species is named for its occurrence in Papua New Guinea.

## Lothygia cordigera, new species

Figs. 7, 10, 11, 18, 19, 25
Description. Dorsal coloration. Head dark red; space between eye-ocelli yellow; antennal segments I-III dark red and IV paler; pronotum and scutellum dark red; clavus and corium dark orange; hemelytral membrane dark brown with the following


Fig. 21. Lothygia papuana, new species.
areas yellow: basal angle, apical margin and external face (in some specimens totally dark brown); connexival segments and abdominal segments orange yellow. Ventral coloration. Bright dark red with following areas bright orange yellow: anterior lobe of metathoracic scent gland and pleural margin of abdominal sternites III to VII; rostral segments I-II dark red and III-IV paler; legs bright dark red to bright orange red with a complete or incomplete ochre ring located on the basal third of tibiae. Structures. Antenniferous tubercles unarmed or with small lateral lobe; tylus apically with a spiny projection, very small and difficult to see; rostrum reaching posterior edge of abdominal sternite VII. Genitalia. Genital capsule. Posteroventral edge heartshape (Fig. 7). Parameres. Figures 10, 11.

Measurements. Male. Length head: 2.12; width across eyes: 1.92 ; interocular space: 1.10; interocellar space: 0.55 ; preocular distance: 1.50 ; length antennal segments: I, 1.40; II, 2.20; III, 1.35; IV, 1.70. Pronotal length: 2.30; width across frontal angles: 1.85; width across humeral angles: 3.95 . Scutellar length: 1.65 ; width: 1.80 . Total body length: 12.10 .

Female. Color. Similar to male. Hemelytral membrane dark to pale brown; connexival segments entirely orange yellow or bicolored with anterior half orange yellow and posterior half black; abdominal segments orange yellow or only with posterior margin of VII and a great portion of VIII and IX dark brown; genital plates bright dark red; paratergite VIII orange yellow or bright dark red. Structures. Rostrum reaching anterior third of abdominal sternite VII; gonocoxae I in caudal view dorsoventrally closed (Figs. 18, 19).

Measurements. Length head: 2.17; width across eyes: 1.95; interocular space: 1.15 ; interocellar space: 0.55 ; preocular distance: 1.48 ; length antennal segments: I, 1.45 ; II, 2.10; III, 1.40; IV, 1.70. Pronotal length: 2.60; width across frontal angles: 1.85; width across humeral angles: 4.50 . Scutellar length: 1.90 ; width: 2.25 . Total body length: 13.32 .

Holotype male. NEW GUINEA: Telefomin, III-IV. 71. A. B. Mirza. Deposited in BPBM.

Paratypes. NEW GUINEA: SE: Woitape (1,550-1,750 mts.), 2-3.XI.65. J. and M. Sedlacek. One male, one female. Deposited in BPBM and IBUNAM. NEW GUINEA: NW: WISSELMEREN: Enarotadi (1,850-1,950 mts.), 19.VII.62. J. Sedlacek. One female. Deposited in BPBM. NEW GUINEA: NE: OKAPA: Purosa (1,700-2,000 mts.), 18.I.66. J. Sedlacek. One male. Deposited in BPBM. NEW GUINEA: NE: TELEFOMIN: Sepik District (1,500 mts.), 18.I.70. A. B. Mirza. One female. Deposited in BPBM. NEW GUINEA: Lower Mist Camp (1,350-1,550 mts.), 31.I.39, 1.II.39, 18.II.39. L. J. Toxopeus (Neth. Ind. American New Guinea Exp.). One male, two females. Deposited in RNHL and IBUNAM.

Discussion. This species resembles L. papuana in appearance, especially in the tylus with its spiny projection. L. cordigera is readily distinguishable by the orange yellow abdominal segments, the heart-shape of the posteroventral edge of the genital capsule and the gonocoxae I dorso-ventrally closed (Fig. 19). In L. papuana the abdominal segments are black, the posteroventral edge of the genital capsule is laterally produced into short blunt lobes (Figs. 4, 7) and the gonocoxae I in caudal view dorso-ventrally opened (Fig. 17).

Etymology: Named for its heart-shaped posteroventral edge of the genital capsule.


## Lothygia enarotadi, new species

Figs. 3, 5, 12, 13, 23
Description. Dorsal coloration. Head black; space between eye-ocelli yellow; antennal segments bright dark red; pronotum pale orange red; scutellum black with apex orange hazel and disc with dark red reflections; clavus and corium pale orange; hemelytral membrane dark brown with basal angle and apical margin yellow; connexival segments orange yellow; abdominal segments I-VI black and VII black with posterior third orange. Ventral coloration. Bright dark red with head bright black and following areas bright yellow: anterior lobe of metathoracic scent gland and pleural margins of abdominal sternites III to VII; rostral segments I-II dark red and III-IV paler; legs bright dark red to bright orange red with a complete or incomplete ochre ring located on the basal third of tibiae. Structures. Antenniferous tubercles with small lateral lobe; tylus apically truncate and globose; rostrum extending beyond posterior edge of abdominal sternite VII (Fig. 3). Genitalia. Genital capsule. Posteroventral edge laterally produced into short blunt lobes and between them a large plate ( 0.70 mm ) (Fig. 5). Parameres. Figures 12, 13.

Measurements. Male. Length head: 2.35; width across eyes: 1.80; interocular space: 1.10; interocellar space: 0.57 ; preocular distance: 1.52 ; length antennal segments: I, 1.55; II, 2.30; III, 1.40; IV, 1.85. Pronotal length: 2.30; width across frontal angles: 2.15; width across humeral angles: 4.15. Scutellar length: 1.95 ; width: 2.10. Total body length: 12.95 .

Female. Color. Similar to male. Scutellum black with apex yellow; abdominal segment VIII black and IX black with orange reflections; genital plates bright dark red; paratergite VIII with or without external edge yellow; connexival segments III to IX yellow with posterior margin black. Structures. Rostrum reaching anterior third of abdominal sternite VII; gonocoxae I in caudal view dorso-ventrally opened.

Measurements. Length head: 2.55; width across eyes: 2.05; interocular space: 1.25; interocellar space: 0.73 ; preocular distance: 1.75 ; length antennal segments: I, 1.67; II, 2.50; III, 1.55; IV, 1.90. Pronotal length: 2.75 ; width across frontal angles: 1.90; width across humeral angles: 5.25 . Scutellar length: 2.40 ; width: 2.75 . Total body length: 15.00 .

Holotype male. NEW GUINEA: NW: WISSELMEREN: Enarotadi (1,800-1,900 mts.), 27.VII.62. J. Sedlacek. Deposited in BPBM.

Paratypes. NEW GUINEA: NW: WISSELMEREN: Enarotadi (1,800-1,900 mts.), 27.VII.62. J. Sedlacek. One female. Deposited in BPBM. NEW GUINEA: Telefomin, III.VI.71. A. B. Mirza. One male. Deposited in BPBM. NEW GUINEA: Sigi Camp ( $1,500 \mathrm{mts}$. ), 22.II.39. L. J. Toxopeus (Neth. Ind. American New Guinea Exp.). One female. Deposited in RNHL. NEW GUINEA: Mist Camp (1,800 mts.), 10-12.I. 39. L. J. Toxopeus. Two males, one female. Deposited in RNHL and IBUNAM.

Discussion. Very close to L. papuana, with abdominal segments I to VI black and gonocoxae I in caudal view dorso-ventrally opened (Fig. 17). In L. enarotadi, the

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Figs. 22-25. Dorsal view of Lothygia spp. 22. L. sandaracine, new species. 23. L. enarotadi, new species. 24. L. papuana, new species. 25. L. cordigera, new species.
tylus is apically globose (Fig. 3), the male rostrum extending beyond posterior edge of abdominal sternite VII and the plate of the posteroventral edge of the genital capsule is longer over 0.70 mm . In L. papuana the tylus apically with a small spiny projection (Fig. 1); the male rostrum reaching posterior edge of abdominal sternite VII and the plate is shorter than 0.60 mm .

Etymology: Named for the type locality; a noun in apposition.

## Lothygia sandaracine, new species

Figs. 2, 6, 14, 15, 22
Description. Dorsal coloration. Head and scutellum black; antennal segments I to IV orange hazel; pronotum dark red with anterior third black; clavus and corium dark orange; hemelytral membrane dark brown; connexival segments orange yellow; abdominal segments I to VI bright orange yellow and VII black with anterior half orange yellow. Ventral coloration. Bright dark red, with head bright black and following areas bright yellow: anterior lobe of metathoracic scent gland and pleural margins of abdominal sternites III to VII; rostral segments orange hazel; legs bright dark red to bright orange red with a complete ochre ring located on the basal third of tibiae. Structures. Antenniferous tubercles unarmed; tylus apically with a small spiny projection; rostrum reaching posterior edge of abdominal sternite VII (Fig. 2). Genitalia. Genital capsule. Posteroventral edge sinuate and laterally poorly exposed (Fig. 6). Parameres. Figures 14, 15.

Measurements. Male. Length head: 2.20; width across eyes: 1.85 ; interocular space: 1.12; interocellar space: 0.55 ; preocular distance: 1.54 ; length antennal segments: I, 1.55; II, 2.30; III, 1.50; IV, 1.75. Pronotal length: 2.30 ; width across frontal angles: 1.75; width across humeral angles: 4.20. Scutellar length: 1.65 ; width: 1.95 . Total body length: 12.88 .

Female. Unknown.
Holotype male. NEW GUINEA: Sigi Camp (1,350 mts.), 28.II.39. L. J. Toxopeus (Neth. Ind. American New Guinea Exp.). Deposited in RNHL.

Discussion. Like L. cordigera, L. sandaracine has the abdominal segments I to VI bright orange yellow. Distinguished by the form of the posteroventral edge of the genital capsule which in L. cordigera is heart-shape (Fig. 7) and in L. sandaracine is sinuate and laterally poorly exposed (Fig. 6).

Etymology: From the Greek sandaracinos, orange colored.

## KEY TO LOTHYGIA SPECIES

1. Abdominal segments I to VI black; gonocoxae I in caudal view dorso-ventrally opened
(Fig. 17)
$1^{\prime}$. Abdominal segments I to VI orange yellow; gonocoxae I in caudal view dorso-ventrally closed (Fig. 19) 3
2. Tylus apically with a short spiny projection (Fig. 1); male genital capsule with posteroventral edge with short median plate ( 0.58 mm ). (Fig. 4) . . L. papuana, new species
$2^{\prime}$. Tylus apically globose, truncate (Fig. 3); male genital capsule with posteroventral edge with large median plate ( 0.70 mm ) (Fig. 5) . . . . . . . . . . . . . . . . . L. enarotadi, new species
3. Male genital capsule with posteroventral edge heart-shape (Fig. 7); frontal angles well developed
L. cordigera, new species

3'. Male genital capsule with posteroventral edge sinuate and laterally poorly exposed (Fig. 6); frontal angles poorly developed (Fig. 2)
L. sandaracine, new species

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# HYDROPTILIDAE (TRICHOPTERA) OF COSTA RICA AND THE NEOTROPICS: SYSTEMATICS OF THE GENUS BYRSOPTERYX FLINT (STACTOBIINI) 

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#### Abstract

The systematics of the genus Byrsopteryx are reviewed. Two previously described species, B. mirifica Flint from Venezuela, the type species of the genus, and B. septempunctata (Flint) from Dominica are redescribed and illustrated. In addition, 11 new species are described and illustrated: B. chaconi, B. cuchilla, B. esparta, B. gomezi, B. solisi, B. tapanti, and B. tica from Costa Rica; B. loja and B. rayada from Ecuador; and B. abrelata and B. espinhosa from Brazil. Keys to species for males and females are presented. The genus is transferred from the Leucotrichiini to the Stactobiini. A species level phylogenetic analysis reveals that the Costa Rican species form a monophyletic group.


Seven undescribed species of the microcaddisfly genus Byrsopteryx Flint were collected recently in Costa Rica by R. W. Holzenthal and his colleagues, during a survey of the country's Trichoptera fauna. This inventory, sponsored by the National Science Foundation, and coordinated through the Costa Rican National Biodiversity Institute, has thus far recorded 445 caddisfly species from the country. The family Hydroptilidae, or microcaddisflies, represents $31 \%$ of the known fauna's species diversity, and $56 \%$ of the Costa Rican microcaddisflies are undescribed.

Additional Byrsopteryx specimens from Ecuador and Brazil (with two new species each) were obtained from the National Museum of Natural History, Smithsonian Institution, made available through the collecting efforts of Dr. Oliver S. Flint, Jr. Examination of the Costa Rican and South American material prompted us to review the genus in its entirety and to prepare this, the third in a series of papers on the Hydroptilidae of Costa Rica and the Neotropics.

The genus was established by Flint (1981) for the Venezuelan species Byrsopteryx mirifica. In the same paper, Alisiotrichia septempunctata Flint, 1968, from Dominica was transferred to Byrsopteryx. We redescribe these two species in the present paper. Earlier, we described the larva of B. mirifica and discussed the phylogenetic placement of the genus within the Leucotrichiini (Holzenthal and Harris, 1992). We suggested then that Byrsopteryx more properly belonged in the Stactobiini. This opinion has been expressed elsewhere (Flint, 1992; Harris and Flint, 1993; Harris and Holzenthal, 1993) and we here formally transfer Byrsopteryx to the Stactobiini. Finally, in the present paper, we discuss the phylogenetic relationships of the species of Byrsopteryx and present a key to males and females.

Types of species described in this paper, as indicated in the text, are deposited in the collections of the National Museum of Natural History, Smithsonian Institution,

Washington, D.C. (NMNH), the University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), the Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica (INBIO), and the Museu de Zoologia, Universidade de São Paulo, Brazil (MZSP) [note: types in the MZSP are on indefinite loan to the NMNH, O. S. Flint, Jr., pers. comm.]. All type material is pinned, unless noted otherwise. In Figures 8-20 of male genitalia, A, B, and C are lateral, dorsal, and ventral views, respectively, of abdominal segments VIII-X; D and E are lateral and ventral views, respectively, of the phallic apparatus. In Figures 21-30 of female genitalia, A is a ventral view of abdominal segments VI-XI, and B is an enlarged, ventral view of the vaginal apparatus.

## Byrsopteryx Flint

Byrsopteryx Flint, 1981:27. Type species: Byrsopteryx mirifica, by original designation.

Diagnosis: Adults: Small, total length $2-3 \mathrm{~mm}$. Easily recognized by prominent white or greenish-white spots (elongated into stripes in one species) on dark fuscous body and forewings (Figs. 3, 4, 6, 7). Coloration: Frons covered with white setae; antennae of some species covered with white setae, otherwise fuscous; mesoscutum laterally with large, oval patches of white setae, often coalescing medially; in some species the legs, especially forelegs, with white setae along anterior edges; forewing with elongate spot at base of medial area, an oval spot along the midcostal border, an oval subapical spot, and in some species a small spot at the apex of the wing. No sexual dimorphism in color. Central area of forewing thickened with distinct "line of weakness" (Flint, 1981) separating a posterobasal area (Fig. 5C); large retinaculum of thick white setae present on under surface of forewing at midlength of somewhat thickened costa, apparently used to couple wings (Fig. 5C inset). Hind wing with patch of hooked setae (frenulum) near midcostal border (Fig. 5C) which engages forewing retinaculum. Venation reduced in both wings. Antennae simple with 1719 segments. Ocelli three. Mesoscutum with transverse suture, metascutellum subpentagonal (Fig. 5A). Tibial spur formula 0, 3, 4 (Fig. 5B).

Male genitalia: Complex, structures often difficult to discern and homologize among the species and related genera. Segment VII without ventromesal process. Segment VIII quadrate, tergum shorter than sternum; long, stout setae usually present ventrolaterally, VIII often with dorsolateral processes (especially Costa Rican species). Segment IX recessed within VIII, with distinct dorsolateral appendagelike processes in most species, which may be bifid. Segment $X$ typically reduced to membranous lobe with only lateral portions sclerotized, but in some species apicoventral portion developed into sclerotized, lyre-shaped process. Inferior appendages typically fused into ventral tubular structure, but absent in some species. Subgenital plate present or absent. Phallic apparatus complex, with wide basal section and cylindrical distal portion often bearing spines or sclerotized processes, middle region of phallic apparatus usually very constricted.

Female genitalia: Segment VI with short ventromesal process in two species, absent in others. Segment VII elongate, sternum often slightly emarginate posteriorly. Segment VIII with pair of elongate lateral apodemes and ring of stout setae posteriorly. Segment IX short, bearing pair of elongate lateral apodemes. Segment X + XI short,

with pair of thin papillae apically. Vaginal apparatus (incorrectly referred to as "bursa copulatrix" by Holzenthal and Harris [1992]) variable among species, but usually with elongate tubular process associated with posterior half and mesal sclerotization.

Larvae: Known only for B. mirifica (Holzenthal and Harris, 1992) and B. chaconi, n. sp. Abdomen laterally compressed, thoracic nota and abdominal tergites heavily sclerotized, especially on abdominal segments VIII and IX. Pronotum anterolaterally with paired depressed areas and pair of short, stout setae. Case purse-like and constructed of silk.

Biology: Larvae are madicolous and crawl, within their portable cases, in the spray and splash zones of small waterfalls and on boulders in small streams (Figs. 1, 2). They probably feed by scraping diatoms and other periphyton from the substrate. Aggregations of pupae are found above the waterline in pits and depressions on the sides of wet bedrock and boulders.

The strikingly colored adults very actively run for short distances, changing direction quickly, over streambed rocks, boulders, and large leaves of low riparian vegetation. Occasionally they quickly stop and freeze in position. When disturbed they deftly fly off to another area. Their contrasting black and white coloration and enlivened movements almost mimic the activity of certain ants. Adults are most active in the bright sunlight at any time of day. They only rarely fly to collecting lights at night and are best collected with an aspirator as they run about on the ground.

## Byrsopteryx abrelata, new species

Figs. 8, 25
The incised posterolateral margin of segment IX of the male and the acutely pointed dorsolateral process of this segment distinguish the species. The circular sclerite of the female vaginal apparatus is distinctive.

Male: Length 3.2-3.3 mm. Antennae with 17 segments. Forewing coloration as in Figure 3, except spots somewhat smaller, rounder, with additional, small patch of white setae at middle of anal border. Legs with white setae. Genitalia as in Figure 8. Segment VIII with tergum shorter than sternum; posterior margin broadly rounded and extended ventrolaterally, emarginate ventrally and bearing short setae. Segment IX recessed within VIII, narrowing anterodorsally in lateral view, deep mesal incision anteriorly in dorsal and ventral views; posteriorly with lateral margin incised and with elongate dorsolateral process, narrowing distally, downturned apically to acute point; in dorsal view lateral process narrow, turned mesally, posterior margin incised. Inferior appendages absent. Segment X narrow, largely membranous, without setae; sclerotized laterally. Subgenital plate in ventral view, wide basally, rounded apically with mesal projection; in lateral view, truncate, with pair of acute, apical points.
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Figs. 1-4. 1, 2. Habitats: 1. Type locality of Byrsopteryx chaconi, n. sp., roadside waterfall and seeps of Río Grande de Terraba, along Panamerican Highway, Puntarenas Province, southeastern Costa Rica. 2. Type locality of Byrsopteryx tapanti, n. sp., waterfall on Quebrada Palmitos, Tapantí National Wildlife Reserve, Cartago Province, central Costa Rica. 3, 4. Byrsopteryx spp., habitus. 3. B. gomezi, n. sp. 4. B. rayada, n. sp.


Figs. 5-7. Byrsopteryx spp. 5. Byrsopteryx mirifica Flint: A, head and thorax, dorsal; B, fore, middle and hind tibiae; C , fore and hind wings; inset, retinaculum. 6. B. chaconi, n . sp., forewing coloration. 7. B. rayada, n. sp., forewing coloration.

Phallic apparatus somewhat simple, wide basally and apically, with narrow, elongate, apically bifid, central spine, in lateral view spine upturned.

Female: Length 3.2-3.5 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 25. Segment VII elongate, sternum with slightly emarginate posterior margin. Segment VIII short and wide, posterior margin slightly emarginate with ring of stout setae; laterally with pair of elongate apodemes extending to posterior of segment VI. Segment IX short, narrow, with lateral apodemes extending to middle


Fig. 8. Byrsopteryx abrelata, n. sp., male genitalia.
of segment VIII. Segment X short, triangular, bearing pair of thin papillae. Vaginal apparatus anteriorly with thin circular sclerite and narrow band with small mesal plate; membranous posteriorly.
Holotype: Male, BRASIL: RIO DE JANEIRO: Nova Friburgo, municipal water supply, 950 m , 24.iv.1977, C. M. and O. S. Flint, Jr. (MZSP). Paratypes: Same locality as holotype, 2 males, 3 females (NMNH), 2 males, 5 females (UMSP) (in alcohol).

Etymology: Portuguese and Spanish for "can-opener," referring to the shape of the dorsolateral process of segment IX of the male.

## Byrsopteryx chaconi, new species

Figs. 6, 9, 26
The shape of the dorsolateral processes and the elongate thickened spines on the ventrolateral margin of male segment VIII are distinctive for B. chaconi as is the simple phallic apparatus, which lacks internal spines. The female vaginal apparatus has a very thin transverse band and thin sinuate lateral sclerites.

Male: Length 2.1-2.8 mm. Antennae with 17 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 9. Segment VIII roughly quadrate, tergum less than half length of sternum; laterally and ventrally with thickened, elongate setae; posterior margin with narrow, attenuated, strongly mesally turned, dorsolateral process, its apex excavated; VIII ventrolaterally with pair of long, stout, dark, spinelike setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, abruptly narrowing distally, bearing elongate basodorsal seta. Inferior appendages fused into narrow, elongate tube, in lateral view thin and slightly downturned. Segment X narrow basally, much broader mesally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally and subapically, pair of thin sclerites apically.
Female: Length 2.2-2.8 mm. Antennae with 19 segments. Coloration as in male. Genitalia as in Figure 26. Abdominal segment VII elongate, sternum with slightly emarginate posterior margin. Segment VIII narrow, posterior margin with ring of stout setae, laterally with pair of elongate apodemes extending to middle of segment VII. Segment IX short, narrow, with lateral apodemes extending to posterior of segment VII. Segment X short, wide basally, narrow distally, bearing pair of thin papillae. Vaginal apparatus with thin transverse band anteriorly, elongate posterior tubular process, slightly widening distally, pair of narrow, sinuate, lateral sclerites.

Holotype: Male, COSTA RICA: PUNTARENAS: roadside seep, route 2, just W km 234, $8.976^{\circ}$ N, $83.299^{\circ} \mathrm{W}, 100 \mathrm{~m}$, 8.iv.1987, Holzenthal, Hamilton, Heyn (NMNH). Paratypes: Same locality as holotype, 4 males, 4 females (UMSP), 1 female (UMSP) (in alcohol); same, except 20.ii.1986, Holzenthal, Morse, Fasth, 6 males, 9 females (UMSP), 2 males, 2 females (NMNH), 2 males, 2 females (INBIO), 30 males, 28 females (UMSP) (in alcohol).

Etymology: Named for Isidro Chacón, lepidopterist with the Museo Nacional de Costa Rica, in recognition of his great assistance and friendship during the junior author's work in Costa Rica.


Fig. 9. Byrsopteryx chaconi, n. sp., male genitalia.


Fig. 10. Byrsopteryx cuchilla, n. sp., male genitalia.

## Byrsopteryx cuchilla, new species

Figs. 10, 27
The knifeshaped dorsolateral processes of segment VIII and the short, thickened spines on the venter of VIII are distinguishing characters of the males of this species. The vaginal apparatus of the female has large oblong lateral plates and a wide transverse band.

Male: Length 2.3-2.7 mm. Antennae with 19 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 10. Segment VIII quadrate, tergum about half length of sternum; laterally and ventrally with thickened elongate setae; posterior margin with knifeshaped lateral process; VIII mesoventrally with pair of short, stout, dark, spinelike setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with sinuate, elongate, dorsolateral process, broad basally and mesally, narrowing distally, elongate basodorsal seta, in dorsal and ventral views dorsolateral process wide for $3 / 4$ length, then narrowing subapically, with small, subapicomesal, acute projection. Inferior appendages fused into elongate thin tube, in lateral view, wide basally, then narrowing to downturned apex. Segment X narrow basally, broader mesally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically, apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus structurally complex, wide basally, mesally and subapically; pair of large, lanceolate sclerites apically.

Female: Length 2.7 mm . Antennae with 19 segments. Coloration as in male. Genitalia as in Figure 27. Segment VII elongate, sternum with slightly emarginate posterior margin. Segment VIII elongate, narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, narrow, with lateral apodemes extending to middle of segment VII. Segment X short, wide basally, narrow distally, bearing pair of thin papillae. Vaginal apparatus with narrow transverse band anteriorly, with elongate, tubular, posterior process, slightly widening distally, laterally with pair of oblong lobes, sclerotized on anterior margins.

Holotype: Male, COSTA RICA: [CARTAGO]: Chitaría, 19.vi.1967, Flint and Ortiz (NMNH). Paratypes: Same locality as holotype, 4 males (NMNH), 1 male (UMSP), 1 male (INBIO), 1 female (NMNH) (in alcohol).

Etymology: Spanish for "knife" or "blade," referring to the distinctive dorsolateral processes from segment VIII of the male genitalia.

## Byrsopteryx esparta, new species

Fig. 11
In many respects, B. esparta is similar to B. cuchilla. Males of both have knifelike dorsolateral processes from segment VIII, but the thickened spines from the ventrolateral margin of this new species are elongate.

Male: Length 2.2-2.4 mm. Antennae with 19 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 11. Segment VIII quadrate, tergum about $1 / 3$ width of sternum; laterally and ventrally with thickened, elongate setae; posterior margin with narrow, knifeshaped, mesally directed, lateral process; VIII ventrolaterally with pair of long, narrow, dark, spinelike setae. Segment IX
recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views, posteriorly with elongate dorsolateral process, narrowing distally, bearing elongate, basodorsal seta; in dorsal view, lateral process wide basally, narrowing distally. Segment X narrow basally, broader mesally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Inferior appendages fused into elongate, narrow tube; in lateral view, wide basally, then narrowing to downturned apex. Subgenital plate absent. Phallic apparatus wide basally, tubular apically, apex with pair of thin, flat sclerites.

Female: Unknown.
Holotype: Male, COSTA RICA: [PUNTARENAS]: 14.1 mi SE Esparta, 23.vii.1967, O. S. Flint, Jr. (NMNH). Paratypes: Same locality as holotype, 11 males (NMNH); Puntarenas: Río Jaba at rock quarry, 1.4 km (air) W Las Cruces, $8.79^{\circ} \mathrm{N}, 82.97^{\circ} \mathrm{W}$, $1,150 \mathrm{~m}$, 9.viii.1990, Holzenthal, Blahnik, Muñoz, 16 males, 1 female (UMSP), 8 males (INBIO) (in alcohol).

Etymology: Named for the type locality, the small town of Esparta, east of the Pacific port city of Puntarenas.

## Byrsopteryx espinhosa, new species

Fig. 12
The prominent dorsolateral process from segment IX with its acute projections and the numerous subapical phallic spines are distinctive features of B. espinhosa. The species is not clearly related to any others in the genus.

Male: Length 3.2 mm . Antennae with 17 segments, covered with white setae. Forewing coloration as in Figure 3, except apical spot larger. Legs, especially forelegs, with white setae along anterior edges. Genitalia as in Figure 12. Segment VIII quadrate, tergum shorter than sternum; posterior margin broadly rounded ventrolaterally, truncate ventrally and bearing long setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views, posteriorly with divided lateral process, its dorsal part elongate and downturned to acute apex, ventral part short and acute; in ventral view, dorsal part spatulate, ventral part short and wide with acute points on inner apical margins. Inferior appendages appear to be absent. Segment X broad, largely membranous, without setae; sclerotized laterally. Subgenital plate truncate in ventral view with small apicomesal projection, in lateral view, oblong in shape, the apicomesal projection downturned. Phallic apparatus structurally complex, wide basally, tubular distally, with dorsolateral sclerotization and numerous subapical spines.

Female: Unknown.
Holotype: Male, BRASIL: RIO DE JANEIRO: km 17, 18 km S Teresopolis, 1,180 m, 18-19.iv.1977, C. M. and O. S. Flint, Jr. (MZSP).

Etymology: Portuguese for "thorny" or "prickly," in reference to the phallic spines.
Byrsopteryx gomezi, new species
Figs. 3, 13, 24
This new species is closely related to the other Costa Rican species. The lack of a prominent dorsolateral process from the posterior margin of male segment VIII and


Fig. 11. Byrsopteryx esparta, n. sp., male genitalia.
the distinctive spinose phallic apparatus serve to distinguish B. gomezi from its relatives. The female is easily distinguished by the large membranous anterior lobes and elongate posterior tubular process of the vaginal apparatus.

Male: Length 2.3-2.5 mm. Antennae with 17 segments. Forewing coloration as in


Fig. 12. Byrsopteryx espinhosa, n. sp., male genitalia.

Figure 3. Legs without white setae. Genitalia as in Figure 13. Segment VIII roughly quadrate, tergum shorter than sternum; posterior margin broadly rounded ventrolaterally and ventrally and bearing many thickened, elongate setae. Segment IX elongate, recessed within segments VIII and VII, acutely narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate sinuate lateral process, broad basally, narrowing distally, bearing elongate seta middorsally. Inferior appendages fused into elongate, narrow tube; in lateral view, thin, slightly downturned. Segment X broad basally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, narrow mesally, distally bearing clump of mesal spines, with pair of elongate, thickened lateral spines, apex divided into pair of long, spinose lobes.

Female: Length 2.3-2.5 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 24. Segment VII elongate. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VI. Segment IX short with lateral apodemes extending to middle of segment VIII. Segment X short, wide basally narrowing apically, bearing pair of thin papillae. Vaginal apparatus with pair of elaborate, membranous lobes anteriorly, oblong mesal plate with elongate tubular process posteriorly.
Holotype: Male, COSTA RICA: PUNTARENAS: Río Bellavista, ca. 1.5 km NW Las Alturas, $8.951^{\circ} \mathrm{N}, 82.846^{\circ} \mathrm{W}, 1,400 \mathrm{~m}, 10-11 . v i i i .1990$, Holzenthal, Blahnik, Muñoz (NMNH). Paratypes: Same locality as holotype, 98 males, 1 female (UMSP). ALAJUELA: Río Peje and falls, ca. 1 km SE San Vicente, $10.277^{\circ} \mathrm{N}, 84.388^{\circ} \mathrm{W}$, 1,450 m, 14-15.ii.1992, Holzenthal, Muñoz, Kjer, 24 males, 2 females (UMSP). CARTAGO: Orosí, Río Tuasito, $1,200 \mathrm{~m}, \mathrm{~L}-\mathrm{N}-196300$, 565200, 14.ix.1991, F. Muñoz, F. A. Quesada, 8 males, 1 female (INBIO). GUANACASTE: Río Aguacate, 0.5 km E Aguacate, $10.565^{\circ} \mathrm{N}, 84.939^{\circ} \mathrm{W}$, 16.ii.1992, Holzenthal, Muñoz, Kjer, 6 females (UMSP).

Etymology: Named for Luís Diego Gómez, eminent Costa Rican biologist, both in honor of his pioneering contributions to our knowledge of Costa Rican natural history and in recognition of his invaluable assistance to the junior author.

## Byrsopteryx loja, new species

Figs. 14, 21
The acute divided lateral process of segment IX and elongate central phallic spine are distinguishing features of male $B$. loja. The female is recognized by the tapered ventral process of segment IX and the shape of the vaginal apparatus, which it shares with $B$. rayada, n. sp.

Male: Length 2.4-3.0 mm. Antennae with 17 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 14. Segment VIII with tergum about half length of sternum; posterior margin narrowly rounded and extended ventrolaterally, bearing long setae; ventally with small, shallow mesal incision. Segment IX recessed within VIII, narrowing anteriorly in lateral view, narrow mesal incision anteriorly in ventral view, posteriorly with divided sclerotized lateral process, divided into dorsal and ventral subprocesses, dorsal subprocess elongate and narrow, with acute, downturned apex, ventral subprocess wide basally with narrow ventral


Fig. 13. Byrsopteryx gomezi, n. sp., male genitalia.


Fig. 14. Byrsopteryx loja, n. sp., male genitalia.
hook, in ventral view this hook thin, directed outward, dorsal subprocess wide, apex narrow, turned mesally. Inferior appendages absent. Segment X broad, largely membranous, narrowing to acute apex; sclerotized laterally. Subgenital plate narrow and oblique in lateral view, rectangular in ventral view. Phallic apparatus somewhat simple, wide basally, tubular distally, with thin elongate central spine and pair of lateral sickle-shaped sclerites.

Female: Length 2.4 mm . Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 21. Segment VI with short ventromesal process. Segment VII about as wide as long. Segment VIII elongate, narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX elongate, narrow, ventrally with tapering process, laterally with pair of elongate apodemes extending to posterior of segment VII. Segment X short, wide basally, narrow distally, bearing pair of thin papillae. Vaginal apparatus structurally simple, thin transverse band and lateral sclerotization anteriorly, posteriorly with membranous foldings.

Holotype: Male, ECUADOR: ZAMORA-CHINCHIPE: 30 km E Loja, 2,000 m, 23.ix.1990, O. S. Flint, Jr. (NMNH). Paratypes: Same locality as holotype, 2 males (NMNH), 1 male (UMSP), 19 males, 1 female (NMNH) (in alcohol).

Etymology: Named for the city of Loja, near the type locality.

## Byrsopteryx mirifica Flint

Figs. 5, 15, 23
Byrsopteryx mirifica Flint, 1981:27, figs. 121-126, male, Venezuela: Aragua, USNM type 76625; Holzenthal and Harris, 1992:405, figs. 1, 2, male, female, larva, case.

Byrsopteryx mirifica is similar in some respects to $B$. loja in that the posterior processes from male segment IX are bifurcate and the phallic apparatus is rather simple, but the two species do not appear to be closely related. The long spinose process from the venter of X is distinctive for the species. The females are easily distinguished by the large mesal plate and the large posterior membranous lobes of the vaginal apparatus.

Redescription: Male: Length 2.3-2.6 mm. Antennae with 17 segments. Transverse white band on head above antennal bases, pair of round white spots on mesoscutum, elongate white spot basally on forewing, oblique spot near midlength, and series of small apical spots around wing margin. Genitalia as in Figure 15. Segment VIII roughly quadrate, tergum about half length of sternum; round and extended ventrolaterally, ventrally with V-shaped mesal incision. Segment IX short, recessed within VIII, rounded anteriorly in lateral view; deep mesal incision anteriorly in dorsal and ventral views, posteriorly with divided lateral processes, each of which is narrow and elongate; in ventral view, these processes appearing chelate. Inferior appendages fused, thin, curving ventrad in lateral view; in ventral view wide basally tapering to thin, downturned apex, curving ventrad. Segment X largely membranous, short; apparently associated with X dorsomesally is a long, thin, gently curved sclerotized process (fused intermediate appendages?). Subgenital plate reduced, represented by pair of mesal crescentric sclerites. Phallic apparatus simple, tubular, narrowing mesally, ejaculatory duct thin with sclerotized apex.

Female: Length 2.4-2.6 mm. Antennae with 17 segments. Coloration as in male.


Fig. 15. Byrsopteryx mirifica Flint, male genitalia.
Genitalia as in Figure 23. Segment VII elongate, sternum incised mesally on posterior margin. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short with lateral apodemes extending to posterior of segment VII. Segment X short, wide, narrowing posteriorly, bearing pair of thin papillae. Vaginal apparatus with pair of large membranous lobes posteriorly; lightly sclerotized mesal plate, with wide mesal excision posteriorly, narrow tongue anteriorly.

Material examined: VENEZUELA: ARAGUA: Parque Nacional Henri Pittier, Río La Trilla, 22.5 km N Rancho Grande on road, 17-19.ix.1979, H. M. Savage, 1 male (NMNH); Maracay, Río Limón, Estacion Piscicultura, 16.ii.1976, C. M. and O. S. Flint, Jr., 25 male paratypes, 10 female paratypes (NMNH).

## Byrsopteryx rayada, new species

Figs. 4, 7, 16, 22
The distinctive white bands on the forewings, the lobate lateral process of segment IX of the male, and the overall large size separate the new species. The vaginal apparatus of the female is simple and most similar to that of B. loja.

Male: 3.2-4.8 mm. Antennae with 17 segments, covered with white setae. Forewing coloration as in Figures 4, 7. Genitalia as in Figure 16. Segment VIII with tergum shorter than sternum; posterior margin broadly rounded and extended ventrolaterally, with V-shaped mesal excavation ventrally and bearing long setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views, posteriorly with elongate lateral process divided into lateral and mesal subprocesses, lateral subprocess broad basally, abruptly narrowing to blunt ventral lobe, mesal subprocess elongate, narrow, with downturned acute apex. Inferior appendages absent. Segment X broad, largely membranous, sclerotized laterally, apex acute and downturned. Subgenital plate absent. Phallic apparatus wide basally, tubular distally, with thin, curving, elongate central spine and membranous apical lobes.

Female: Length 3.8 mm . Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 22. Segment VI with short ventromesal process. Segment VII quadrate. Segment VIII elongate, narrow, posterior margin with ring of stout setae, laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, wide, deeply incised ventrally, with pair of elongate mesal apodemes extending to posterior of segment VII. Segment X short, wide basally, narrow distally, with pair of thin papillae. Vaginal apparatus structurally simple, with thin transverse band anteriorly, posteriorly with membranous foldings, tapered distally.

Holotype: Male, ECUADOR: CAÑAR: Río Chauchas, 3 km N Zhud, 2,910 m, 17.ix.1990, O. S. Flint, Jr. (NMNH). Paratypes: Same locality as holotype, 17 males, 1 female (NMNH), 2 males (UMSP), 2 males (NMNH) (in alcohol).

Etymology: Spanish, meaning "having stripes" and referring to the distinctive, striped forewings.

## Byrsopteryx septempunctata (Flint)

Fig. 17
Alisiotrichia septempunctata Flint, 1968:46, figs. 106-109, male, Dominica: Pont Casse, USNM Type 69898; Byrsopteryx septempunctata, Flint, 1981:27.

Byrsopteryx septempunctata is distinguished by its combination of genitalic features, including the inferior appendages which are fused into a thin elongate tubular process, the venter of segment X which is less developed than in many Byrsopteryx species, and the paired lateral processes of segment IX. It seems to be the sister species of the Costa Rican clade.


Fig. 16. Byrsopteryx rayada, n. sp., male genitalia.


Fig. 17. Byrsopteryx septempunctata (Flint), male genitalia.

Redescription: Male: Length 2.6 mm . Antennae with 17 segments. Forewing coloration as in Figure 6, except spots bright green. Genitalia as in Figure 17. Segment VIII quadrate, tergum shorter than sternum; posterior margin rounded ventrolaterally, ventrally with $V$-shaped mesal incision; bearing many long setae. Segment IX elongate, recessed within VIII, narrowing anteriorly in lateral view; deep mesal incision anteriorly in dorsal and ventral views; posteriorly with pair of thin lateral processes, upper process upturned, lower process downturned, in ventral view upper process more lateral in position, narrow and acute apically, lower process mesad in position, sinuate distally. Inferior appendages fused into elongate, narrow tube, membranous laterally; in lateral view, thin, upturned apically. Segment X membranous anterodorsally, posteriorly with sclerotized lateral bands; venter sclerotized. Subgenital plate absent. Phallic apparatus wide basally, narrow mesally, cylindrical distally with 6-7 elongate, curved, internal spines.

Female: Unknown.
Material examined: DOMINICA: Pont Casse, 2.2 mile east, 14.iv.1964, O. S. Flint, Jr., holotype male, USNM Type 69898.

## Byrsopteryx solisi, new species

Figs. 18, 28
The truncate dorsolateral process and the four thick elongate spines from the ventromesal margin of segment VIII are distinguishing male characteristics for this species. The female vaginal apparatus has an elongate posterior tubular process, small oblong lateral plates, and a wide transverse band.

Male: Length 2.4-2.8 mm. Antennae with 19 segments. Forewing coloration as in Figure 3. Legs without white setae. Genitalia as in Figure 18. Segment VIII quadrate, tergum shorter than sternum; posterior margin with broad, blunt, dorsolateral process; ventrolaterally with thickened, elongate setae; mesoventrally VIII somewhat narrowed distally and bearing 4 stout, dark, spinelike setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, narrowing and downturned distally, bearing elongate seta basodorsally. Inferior appendages fused into short tube; in ventral view wide basally, slightly tapering distally; in lateral view thin, gently downturned. Segment X narrow basally, broader mesally; membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, very narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, tubular distally, bearing pair of large, lanceolate spines apicoventrally.

Female: Length 2.6-3.1 mm. Antennae with 19 segments. Coloration as in male. Genitalia as in Figure 28. Segment VII elongate, sternum slightly emarginate on posterior margin. Segment VIII narrow, posterior margin emarginate with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short with lateral apodemes extending to middle of segment VIII. Segment X short, widest mesally, bearing pair of thin papillae. Vaginal apparatus with narrow transverse band mesally, tubular processes posteriorly, pair of lightly sclerotized oblong plates laterally, truncate anteriorly.

Holotype: Male, COSTA RICA: PUNTARENAS: Río Singrí, 2 km (air) S Finca


Fig. 18. Byrsopteryx solisi, n. sp., male genitalia.

Helechales, $9.057^{\circ} \mathrm{N}, 83.082^{\circ} \mathrm{W}, 720 \mathrm{~m}, 21 . \mathrm{ii} .1986$, Holzenthal, Morse, Fasth (NMNH). Paratypes: Same locality as holotype, 26 males, 16 females (UMSP). ALAJUELA: Río Sarapiquí, ca. 2 km SE Cariblanco, $10.299^{\circ} \mathrm{N}, 82.172^{\circ} \mathrm{W}, 710 \mathrm{~m}$, 22.vi.1986, Holzenthal, Heyn, Armitage, 3 males, 1 female (INBIO). GUANACASTE: Río Aguacate, 0.5 km E Aguacate, $10.565^{\circ} \mathrm{N}, 84.939^{\circ} \mathrm{W}$, 16.ii.1992, Holzenthal, Muñoz, Kjer, 1 male (UMSP). HEREDIA: Río Bijagual on road to Magsasay, $10.408^{\circ} \mathrm{N}, 84.076^{\circ} \mathrm{W}$, 140 m, 12.ii.1986, Holzenthal, Morse, Fasth, 1 male (NMNH). PUNTARENAS: Río Guineal, ca. 1 km (air) E Finca Helechales, $9.076^{\circ} \mathrm{N}, 83.092^{\circ} \mathrm{W}, 840 \mathrm{~m}$, Holzenthal, Morse, Fasth, 18 males, 7 females (UMSP).

Etymology: Named in honor of Angel Solís, curator of Coleoptera and head of the Department of Entomology, Instituto Nacional de Biodiversidad, Costa Rica, who has been instrumental in the initial and continued success of the junior author's research in Costa Rica.

## Byrsopteryx tapanti, new species

Figs. 19, 29
The elongate, narrow dorsolateral processes and pair of thickened spines from the ventrolateral margin of segment VIII are distinctive for males of B. tapanti. The female vaginal apparatus has a thin, sinuate posterior process originating from an oblong mesal plate.

Male: Length 2.7-3.0 mm. Antennae with 17 segments. Forewing coloration as in Figure 3. Legs without white setae. Genitalia as in Figure 19. Segment VIII roughly quadrate, tergum less than half length of sternum; posterior margin with thin, elongate dorsolateral process, sharply bent downward at apex, curved inward when viewed ventrally; ventrolaterally with pair of long, stout spines, slightly curved inward apically; mesoventrally with pair of thin spines, these sinuate in lateral view, straight in ventral view; VIII laterally and ventrally with thickened, elongate setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, narrowing and downturned distally, bearing elongate seta basodorsally. Inferior appendages fused into narrow, elongate tube; in lateral view thin, gently downturned. Segment X narrow basally, broader mesally; membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, tubular distally, bearing pair of spines apicoventrally and semimembranous, coneshaped mesal protuberance.

Female: Length 2.7-3.0 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 29. Segment VII elongate, sternum slightly emarginate on posterior margin. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, narrow, with lateral apodemes extending to posterior of segment VII. Segment X short, widest mesally, bearing pair of thin papillae. Vaginal apparatus with thin, sinuate, transverse band anteriorly, oblong mesal plate bearing thin, elongate, tubular process posteriorly.

Holotype: Male, COSTA RICA: CARTAGO: Res. Tapantí, Quebrada Palmitos and falls, $9.72^{\circ} \mathrm{N}, 83.78^{\circ} \mathrm{W}, 1,400 \mathrm{~m}, 24-25 . i i i .1991$, Holzenthal, Muñoz, Huisman


19E


Fig. 19. Byrsopteryx tapanti, n. sp., male genitalia.
(NMNH). Paratypes: Same locality as holotype, 42 males, 1 female (UMSP); same, except 1-2.viii. 1990, Holzenthal, Blahnik, Muñoz, 1 female (INBIO); same, except waterfall ca. 1 km (road) NW tunnel, $9.69^{\circ} \mathrm{N}, 83.76^{\circ} \mathrm{W}, 1,600 \mathrm{~m}, 24 . \mathrm{iii} .1991$, Holzenthal, Muñoz, Huisman, 1 female (UMSP); same, except Q. Salto [=Q. Palmitos], 12.ix.1991, L-N-190650, 560000, F. Muñoz \& F. A. Quesada, 2 males (INBIO).

Etymology: Named for the type locality, the Tapantí wildlife refuge near the town of Orosi, Cartago Province.

Byrsopteryx tica, new species
Figs. 20, 30
The thickened, curved spines from the posterior margin of male segment VIII are distinctive for $B$. tica. The female vaginal apparatus has a narrow transverse sclerite and elongated tubular process projecting posteriorly.

Male: Length 2.8-3.0 mm. Antennae with 17 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 20. Segment VIII roughly quadrate, tergum less than half length of sternum; posterior margin with elongate dorsolateral process, downturned and sharply turned inward apically; ventrolaterally with pair of long, stout spines, strongly curved outward apically; VIII laterally and ventrally with thickened, elongate setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, narrowing and downturned distally, bearing elongate seta basodorsally. Inferior appendages fused into narrow, elongate tube; in lateral view thin, gently downturned. Segment X narrow basally, broader mesally; membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, mesally, and subapically, bearing pair of spines apicoventrally and pair of membranous lobes apically.

Female: Length 2.8-3.0 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 30. Segment VII elongate, sternum truncate on posterior margin. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, narrow, with lateral apodemes extending to middle of segment VII. Segment X short, wide basally, narrowing to rounded apex, bearing pair of thin papillae. Vaginal apparatus with narrow transverse band anteriorly, elongate, tubular process posteriorly, widest basally and apically.

Holotype: Male, COSTA RICA: CARTAGO: Res. Tapantí, unnamed trib., ca. 8 km (rd.) S headquarters, $9.76^{\circ} \mathrm{N}, 83.78^{\circ} \mathrm{W}, 1,540 \mathrm{~m}, 24 . i i i .1991$, Holzenthal, Muñoz, Huisman (NMNH). Paratypes: Same locality as holotype, 14 males, 2 females (UMSP), 1 male (INBIO), 1 male (NMNH).
Etymology: Named for the Costa Ricans, or "Ticos."

## PHYLOGENETIC ANALYSIS

Methods. The computer program PAUP, version 3.1.1 (Swofford, 1993) was used to infer the phylogenetic relationships of the species of Byrsopteryx. The application was run on a Macintosh Centris $610{ }^{\circledR}$ microcomputer with 16 MB of RAM. Nineteen characters from larval and adult stages were included in the analysis. Characters were


Fig. 20. Byrsopteryx tica, n. sp., male genitalia.
Table 1. Character matrix for Byrsopteryx species.

| Taxa | Character |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| Celaenotrichia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| abrelata | ? | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| chaconi | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 0 |
| cuchilla | ? | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| esparta | ? | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? |
| espinhosa | ? | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | ? | ? | ? |
| gomezi | ? | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| loja | ? | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| mirifica | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| rayada | ? | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| septempunctata | ? | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? | ? | ? | ? |
| solisi | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| tapanti | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 |
| tica | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |

Characters $(0=$ plesiomorphic state; $1,2=$ apomorphic states; ? = missing data): Larval Character: Character 1:0 = larval pronotum normal; $1=$ larval pronotum with lacunate areas and with strong apicolateral seta. Adult Characters: Character $2: 0=$ forewing not punctate; $1=$ forewing with bright white spots. Character 3: $0=$ wing venation normal; $1=$ wing venation reduced. Character $4: 0=$ forewing without fracture; $1=$ forewing with fracture. Character 5: $0=1,3,4$ tibial spur formula; $1=0,3,4$ tibial spur formula. Male Genitalia: Character $6: 0=$ segment VII with ventromesal process; $1=$ segment VII without ventromesal process. Character 7: $0=$ segment VIII without long thick setae ventrally; segment VIII with long thick setae ventrally. Character 8: $0=$ segment VIII without dorsolateral process; $1=$ segment VIII with dorsolateral process; $2=$ segment VIII dorsolateral process bladelike. Character $9: 0=$ segment VIII without thick, spinelike mesoventral setae; $1=$ segment ind single, sinuate posterolateral appendagelike process; $2=$ segment IX posterolateral appendagelike process single, sinuate, and with dorsal seta. haracter $11: 0=$ segment $X$ unmodified; $1=$ segment $X$ with lyre-shaped sclerotization. Character $12: 0=$ inferior appendages absent; $1=$ 14: $0=$ segment VI with ventromesal process; $1=$, plate; $1=$ vaginal apparatus with mesal plate. Character $16: 0=$ vaginal posterior tubular process. Character 17: $0=$ vaginal apparatus without transverse band; $1=$ vaginal apparatus with transverse band; $2=$ vaginal apparatus transverse band sinuate. Character 18: $0=$ vaginal apparatus without lateral plates; $1=$ vaginal apparatus with lateral plates. Character 19: $0=$ vaginal apparatus rounded or oval; $1=$ vaginal apparatus diamond-shaped.
entered as " 0 " if ancestral and as " 1 " or " 2 " if derived, depending on the number of derived states. All characters were equally weighted and considered nonadditive. Celaenotrichia edwardsi was designated as the outgroup taxon.

Character analysis and polarization. Character 1. Larval pronotum with lacunate areas and with stout apicolateral seta (Holzenthal and Harris, 1992: fig. 1A, B). In separate papers, we suggested that the monobasic Chilean genus Celaenotrichia was closely related to Byrsopteryx (Harris and Holzenthal, 1993; Harris and Flint, 1993). The larvae of Celaenotrichia edwardsi are very similar to known Byrsopteryx larvae in overall morphology and ecology, however, the modified pronotum of Byrsopteryx is unique to the genus. Larvae of only $B$. mirifica and $B$. chaconi are known. Celaenotrichia has an unmodified pronotum, representing the ancestral condition seen in other Hydroptilidae.

Character 2. Forewing with bright white spots made of setae (stripes in B. rayada) on a dark fuscous background (Figs. 3, 4, 6, 7). While other hydroptilids have patterns of colored setae and scales on the forewings, we know of no other genus which has such brightly contrasting spots. Furthermore, its bright color pattern coupled with its active diurnal behavior and madicolous habitat render Byrsopteryx unique, at least among all other Stactobiini in Costa Rica, where we have many field observations. The structure of the retinaculum and frenulum of Byrsopteryx may also be synapomorphic, but we have not investigated these structures in other stactobiines.

Character 3. Forewing venation reduced to only a few longitudinal veins and Character 4: forewing with fracture (Fig. 5C). This combination of characters is derived when compared to the more complete pattern of wing venation seen in Celaenotrichia. However, other stactobiine genera have varying degrees of reduced venation and some have what appear to be fractures or sutures in the forewing (Harris, unpubl. data). The homology of these venational patterns will be presented by Harris and O. S. Flint, Jr., in a review of the Neotropical Stactobiini. The wing venation in Byrsopteryx might represent a more generally distributed stactobiine pattern.

Character 5. Tibial spur formula 0, 3, 4 (Fig. 5B). The primitive distribution of tibial spurs in the Trichoptera is 2 on the foretibia, 4 on the middle tibia, and 4 on the hind tibia, giving a spur formula of $2,4,4$. Spur formula in Celaenotrichia is 1 , 3, 4 and in Byrsopteryx, 0, 3, 4. Losses of tibial spurs occur frequently throughout the Trichoptera and especially so in the Hydroptilidae, thus the possibility of homoplasy with other stactobiine genera is high.

Character 6. Male abdominal segment VII without ventromesal process. The presence of a small spurlike process on sternum VII (or VI or both) is part of the ground plan of the Trichoptera. Its absence is derived, but again, this is a loss that occurs frequently throughout the order. Celaenotrichia edwardsi possesses a prominent ventromesal process. Its loss in male Byrsopteryx is derived.

Character 7. Male abdominal segment VIII with long thick setae ventrally (Figs. 9A, 10A). This character state, shared by all of the Costa Rican species, is derived. Abdominal setae in Celaenotrichia and other Byrsopteryx are shorter and more slender.

Character 8. Male abdominal segment VIII with dorsolateral processes (Figs. 9A, 10A). These processes, found in all of the Costa Rican species except B. gomezi, are derived. The bladelike condition seen in B. cuchilla and B. esparta is a further derived condition. These processes are lacking in Celaenotrichia and other Byrsopteryx species.

Character 9. Male abdominal segment VIII with thick spinelike mesoventral (and ventrolateral) setae (Figs. 9C, 10C). These modified setae are found only in B. chaconi, B. cuchilla, B. esparta, B. solisi, B. tapanti, and B. tica. They are derived.

Character 10. Male abdominal segment IX with posterolateral appendagelike processes (Figs. 8A, 9A, 12A, 14A, 16A, 17A). This character is variable within the genus and we are uncertain if the structures are even homologous among the species. The character was coded as multistate, depending on whether the processes were bifid, single and sinuate, or single, sinuate, and with a dorsal seta. The bifid condition was coded as primitive since that is the condition in Celaenotrichia. We are especially uncertain about the homology of the bifid condition. Within the bifid state, it is difficult to determine if the process is a single basally bifid structure, or if the process is in fact two separate processes, closely associated basally. Other stactobiines, and some Alisotrichia species, have processes located dorsolaterally on segment IX. We do not know if these various structures represent homologies or homoplasies. We are certain that these processes in the Costa Rican species are synapomorphic, because they are very similarly shaped, positioned, and each bears a similarly positioned dorsal seta.

Character 11. Male abdominal segment X with lyre-shaped sclerotization (Fig. 9A, B). The details of structure and shape of segment X in the Costa Rican species indicate synapomorphy. Segment $X$ in the outgroup and other species is not modified in such a way, but there are differences in the morphology of this segment among the other species. We have not analyzed the phylogenetic significance of these differences.

Character 12. Male inferior appendages (Fig. 9A, C). Separate, ventrolateral inferior appendages are part of the ground plan of the Trichoptera. None of the modifications in Byrsopteryx are "typical" trichopteran inferior appendages. We are not certain that the tubular structures seen in some Byrsopteryx are homologous with inferior appendages, but their ventral position on segment IX is consistent with the position of inferior appendages. The tubular structure may represent a highly modified subgenital plate or an altogether new structure. We have seen no intermediate states between the tubular condition and the typical separate condition. Celaenotrichia lacks inferior appendages. The absence of interior appendages was considered the plesiomorphic state and the presence of tubular structures the apomorphic state.

Character 13. Male subgenital plate absent. The subgenital plate is part of the ground plan of the Hydroptilidae. Its absence is considered derived.

Character 14. Female abdominal segment VI without ventromesal process (see discussion under character 6.)

Character 15. Female vaginal apparatus with mesal plate (Figs. 23B, 24B, 25B). This structure is not seen in Celaenotrichia and Alisotrichia in the Stactobiini nor in Leucotrichia in the Leucotrichiini. Its presence in several Byrsopteryx species is cautiously considered derived. Homology and morphology of female Hydroptilidae genitalic structures are less well known than those of the male. Our interpretations of this character and those discussed below are highly tentative.

Character 16. Vaginal apparatus with posterior tubular process (Figs. 24B, 26B, 27B, 28B, 29B, 30B). Of all the female characters this one seems to be the strongest synapomorphy. A similar structure is not known in other Stactobiini.

Character 17. Vaginal apparatus with transverse bands (Figs. 27B, 28B), Character 18: vaginal apparatus with lateral plates (Figs. 27B, 28B), and Character 19: vaginal apparatus diamond-shaped, narrowed anteriorly and posteriorly (Figs. 21B, 22B).


Figs. 21-23. Byrsopteryx spp., female genitalia. 21. B. loja, n. sp. 22. B. rayada, n. sp. 23. B. mirifica Flint.


Figs. 24-26. Byrsopteryx spp., female genitalia. 24. B. gomezi, n. sp. 25. B. abrelata, n. sp. 26. B. chaconi, n. sp.


Figs. 27, 28. Byrsopteryx spp., female genitalia. 27. B. cuchilla, n. sp. 28. B. solisi, n. sp.

The absence of these bands and plates, i.e., a more simple, fully membranous vaginal apparatus and a more oval or rounded vaginal apparatus, is considered the ancestral condition. The sinuate transverse band of the vaginal apparatus seen in B. chaconi and B. tapanti is a further derived condition.

Results and discussion. Six equally parsimonious trees were found using PAUP's BRANCH and BOUND tree searching routine with the COLLAPSE option in effect. It took 0.87 seconds to complete the search. Each tree had a length of 25 steps (minimum $=22$, maximum $=73$ ), consistency index of 0.880 , and retention index of 0.941 . Other indices are given in Figure 31. Identical character distributions were obtained under both ACCTRAN and DELTRAN optimizations. The position of only one terminal taxon, B. espinhosa, changed among the six trees. Excluding this species from the analysis resulted in a single most parsimonious resolution. Strict,


Figs. 29, 30. Byrsopteryx spp., female genitalia. 29. B. tapanti, n. sp. 30. B. tica, n. sp.
semistrict, Adams, and 50\% majority rule consensus trees of the 6 most parsimonious trees had the following tree lengths and C.I.'s respectively: $29,0.759 ; 27,0.815 ; 25$, 0.880 ; and $25,0.880$. Adams and $50 \%$ majority rule consensus trees had identical topologies, equal to one of the most parsimonious trees, and the latter was chosen as the solution tree (Fig. 31). Characters 13, 15, and 17 exhibited homoplasy on the tree. All characters are distributed on the tree as illustrated in Figure 31. Because of our limited information about the fundamental nature of structures in Byrsopteryx we chose not to manipulate the data set by weighting or ordering characters.

Our hypothesis of the phylogeny of the species of Byrsopteryx is presented in Figure 31. Characters 1-6 support the hypothesis that Byrsopteryx is monophyletic. Within the tree, a basal trichotomy exists between B. espinhosa, B. loja $+B$. rayada, and a clade of all other species. Character 19 (vaginal apparatus diamond-shaped) indicates a sister group relationship between $B$. rayada and B. loja. Characters 14 (females without ventromesal process) and 15 (vaginal apparatus with mesal plate) support


Fig. 31. Phylogeny of the species of Byrsopteryx based on $50 \%$ majority rule consensus tree of 6 equally parsimonious trees. Percentages at nodes refer to percent of the 6 parsimonious trees containing that particular clade (all clades $100 \%$ unless otherwise indicated). Numbers to the right of symbols refer to characters and their states as presented in Table 1.
monophyly of all the species, except B. espinhosa, B. loja, and B. rayada, although the latter character is lost in all but two of the Costa Rican species. Character 12 (inferior appendages fused, tubular) supports monophyly for B. mirifica, B. septempunctata, and a clade containing all the Costa Rican species. Character 16 (vaginal apparatus with posterior tubular process) supports monophyly for B. septempunctata and the seven Costa Rican species, although the character is equivocal in B. septempunctata since the females of that species are unknown. Absence of the subgenital plate (Character 13) occurs in B. septempunctata + Costa Rican clade and its loss appears as a convergence in B. rayada. All of the Costa Rican species form a very homogeneous clade defined by character 7 (segment VIII with long thick setae ventrally) and character 11 (segment X with lyre-shaped sclerotization). State 2 of character 10 (segment IX posterolateral appendagelike process single, sinuate, and with dorsal seta) is also synapomorphic for the Costa Rican clade. State 1 of character 10 occurs as an autapomorphy in B. abrelata. Within the Costa Rican species all but B. gomezi share character 8 (segment VIII with dorsolateral processes) and character 9 (segment VIII with thick spinelike mesoventral setae). Character 17 (vaginal apparatus with sinuate transverse bands) is, in its most derived condition (state 2), shared by two of the Costa Rican species, but is considered to revert to state 1 in the remaining four Costa Rican species (Fig. 31). The latter character state appears as an evolutionary convergence in B. loja and B. rayada. Character 18 (vaginal apparatus with lateral plates) supports monophyly of five of the Costa Rican species. State 2 of character 8 (segment VIII dorsolateral processes bladelike) indicates a sister-group relationship between B. cuchilla and B. esparta.

This first assessment of the phylogenetic relationships of the species of Byrsopteryx should be considered very tentative. We have questions about the homology of many structures and our decisions on character polarity are open to reinterpretation. We are more certain, however, that Byrsopteryx is a monophyletic genus, that it belongs in the Stactobiini, and that within it the seven Costa Rican species form a well defined clade. The discovery of additional species, especially from South America, and the female of B. espinhosa will aid future analyses.

The Neotropical Hydroptilidae are a terra incognita in terms of both descriptive taxomony and phylogenetics (Flint, 1992). While many hundreds of species have been described, hundreds more await discovery and description. Each new discovery provides information that has changed and will continue to change our views about the phylogenetic relationships within this most interesting family.

## KEY TO MALE BYRSOPTERYX SPECIES



- Inferior appendages absent (Figs. 8A, 14A, 16A) or, if fused, not into an elongate, narrow tube (Fig. 15A, C); margins of segment VIII without such setae
2 Abdominal segment VIII with dorsolateral process (Figs. 9, 10, 11 18); with stout spinelike setae ventrolaterally and/or mesoventrally on segment VIII (Figs. 9C, 10C, 18C, 19C)
- Abdominal segment VIII without dorsolateral process; lacking stout spinelike setae on segment VIII (Figs. 8C, 14C, 16C)

3 Dorsolateral process of segment VIII broad, blunt apically (Fig. 18A); four stout, dark, spinelike setae mesoventrally on segment VIII (Fig. 18C); fused inferior appendages short in ventral view (Fig. 18C)

Byrsopteryx solisi

- Dorsolateral process of segment VIII narrow, acute apically (Figs. 9A, 10A, 11A, 19A, 20A); two stout, dark, spinelike setae mesoventrally on segment VIII (Figs. 9C, 10C, $11 \mathrm{C}, 19 \mathrm{C}, 20 \mathrm{C}$ ); fused inferior appendages elongate in ventral view (Figs. 9C, 10C, 11C, 19C, 20C)
4 Dorsolateral process of segment VIII short or elongate, downturned apically (Figs. 9A, 19A, 20A), in ventral view, curving inward distally (Figs. 9C, 19C, 20C); spinelike setae of segment VIII elongate, straight, or divergent (Figs. 9C, 19C, 20C)
- Dorsolateral process of segment VIII elongate, straight, knifelike (Figs. 10A, 11A), in ventral view, only slightly curving inward (Figs. 10C, 11C); spinelike setae of segment VIII elongate (Fig. 11C) or short, convergent (Fig. 10C)
5 Dorsolateral process of segment VIII short (Fig. 9A), in ventral view abruptly curving inward apically, broadly shouldered basally (Fig. 9C); phallic apparatus lacking thin, lateral spines (9E)

Byrsopteryx chaconi

- Dorsolateral process of segment VIII elongate (Figs. 19A, 20A), in ventral view gradually curving inward apically, slightly shouldered basally (Figs. 19C, 20C); phallic apparatus with thin, lateral spines (Figs. 19E, 20E) 6
6 Posterior margin of segment VIII with ventrolateral and mesoventral spinelike setae (Fig. 19A), mesoventral pair thin, straight, parallel (Fig. 19C) ...... Byrsopteryx tapanti
- Posterior margin of segment VIII with only mesoventral spinelike setae (Fig. 20A), these thick, widely separated basally, convergent subapically, curving abruptly outward apically (Fig. 20C)
. Byrsopteryx tica
7 Spinelike setae of segment VIII elongate (Fig. 11C); apex of phallic apparatus with thin, flat sclerites (Fig. 11D) ......................................... Byrsopteryx esparta
- Spinelike setae of segment VIII short (Fig. 10C); apex of phallic apparatus with pair of large, lanceolate sclerites (Fig. 10D, E) ............................ Byrsopteryx cuchilla
8 Segment IX with pair of thin lateral processes (Fig. 17A); inferior appendages membranous laterally (Fig. 17C); phallic apparatus with 5-6 elongate, internal spines (Fig. 17D, E)

Byrsopteryx septempunctata

- Segment IX with single, elongate, sinuate, lateral process (Fig. 13A); inferior appendages not membranous laterally (Fig. 13C); phallic apparatus with very many mesal and apical spines (Fig. 13D, E)

Byrsopteryx gomezi
9 Segment IX incised posterolaterally (Fig. 8A); dorsolateral process of segment IX entire (Fig. 8A); phallic apparatus with elongate central spine (Fig. 8D) . . Byrsopteryx abrelata

- Segment IX entire posterolaterally; dorsolateral process of segment IX with dorsal and ventral or mesal and lateral subprocesses; phallic apparatus with single, elongate central spine or numerous spines
10 Dorsal subprocess of segment IX process elongate, acute, in ventral view spatulate; ventral subprocess short, acute, in ventral view wide (Fig. 12A, C); subgenital plate truncate, distinct (Fig. 12A, C); phallic apparatus with numerous subapical spines (Fig. 12D, E)

Byrsopteryx espinhosa

- Dorsal subprocess of segment IX process not spatulate, ventral subprocess narrow in ventral view; subgenital process narrow or absent; phallic apparatus with single, elongate central spine
11 Dorsal and ventral subprocesses of segment IX rounded apically or wide (Fig. 16A), in ventral view, lower subprocesses wide basally, rounded apically (Fig. 16C); subgenital plate distinct (Fig. 16C); forewings with white stripes (Fig. 7) ....Byrsopteryx rayada
- Dorsal and ventral subprocesses of segment IX narrow, acute apically (Figs. 14A, 15A), in ventral view, lower subprocess thin over entire length, acute apically (Figs. 14C, 15 C ); subgenital plate indistinct or reduced; forewings with spots

12 Segment $X$ with elongate, thin sclerotized process from venter (Fig. 15A, B); dorsal and ventral subprocesses from segment IX thin (Fig. 15A, C); inferior appendages present, although fused (Fig. 15A, C)

Byrsopteryx mirifica

- Segment $X$ lacking elongate process from venter (Fig. 14); dorsal subprocess of segment IX wider than ventral subprocess (Fig. 14B); inferior appendages absent

Byrsopteryx loja

## KEY TO FEMALE BYRSOPTERYX SPECIES <br> (females of esparta, espinhosa, and septempunctata not known)

1 Abdominal segment VI with short ventromesal process (Figs. 21A, 22A) .............. 2

- Abdominal segment VI without ventromesal process ..................................... 3

2 Forewings with white bands (Fig. 7); segment IX incised ventrally (Fig. 22A); vaginal apparatus without lateral sclerotization anteriorly (Fig. 22B) ..........Byrsopteryx rayada

- Forewings without white bands; segment IX with ventral tapered process (Fig. 21A); vaginal apparatus with lateral sclerotization anteriorly (Fig. 21B) ....... Byrsopteryx loja
3 Vaginal apparatus with posterior tubular process (Figs. 24B, 26B, 27B, 28B, 29B, 30B)
4
- Vaginal apparatus without posterior tubular process ............................................... 9

4 Vaginal apparatus without transverse sclerite, but with oblong mesal plate (Fig. 24B); large membranous lobes anteriorly (Fig. 24B) ......................... Byrsopteryx gomezi

- Vaginal apparatus with transverse sclerite anteriorly (Figs. 26B, 27B, 28B, 29B, 30B); without membranous lobes anteriorly 5
5 Vaginal apparatus with very thin transverse band (Fig. 26B); posterior mesal process gradually widening distally; laterally with thin sinuate sclerites ..... Byrsopteryx chaconi
_ Vaginal apparatus with wider transverse band (Figs. 27B, 28B, 29B, 30B); posterior mesal process narrowing at midlength or uniformly narrow 6

6 Vaginal apparatus with posterior process uniformly narrow and originating from an oblong plate (Fig. 29B); transverse band sinuate ..................... Byrsopteryx tapanti

- Vaginal apparatus with posterior process narrowing at midlength and not originating from an oblong plate (Figs. 25B, 26B, 30B); transverse band curved, but not sinuate7

7 Vaginal apparatus with short oblong lateral plates (Figs. 27B, 28B); transverse band extending from side to side8

- Vaginal apparatus with long oblong lateral plates (Fig. 30B); transverse band not ex-

8 Vaginal apparatus oblong lateral plates large (Fig. 27B) ............... Byrsopteryx cuchilla
- Vaginal apparatus oblong lateral plates small (Fig. 28B) ................ Byrsopteryx solisi

9 Vaginal apparatus with pair of large, posterior membranous lobes (Fig. 23B); without thin circular sclerite anteriorly and with large mesal plate ........... Byrsopteryx mirifica

- Vaginal apparatus membranous posteriorly, but without large, posterior membranous lobes; with thin circular sclerite anteriorly and with small mesal plate (Fig. 25B)

Byrsopteryx abrelata

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# A GENERIC CONSPECTUS OF THE TRIBE PROCLETICINI PENNINGTON (HETEROPTERA, PENTATOMIDAE), WITH THE DESCRIPTION OF PARODMALEA RUBELLA, NEW GENUS AND SPECIES 

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#### Abstract

The definition of Procleticini is broadened to include a total of eleven genera: Aleixus McDonald, Brepholoxa Van Duzee, Dendrocoris Bergroth, Lobepomis Berg, Neoderoploa Pennington, Odmalea Bergroth, Parodmalea, new genus, Procleticus Berg, Terania Pirán, Thoreyella Spinola, and Zorcadium Bergroth. Characters which unite these genera into a homogeneous group are those involving both the male and female genitalia. Parodmalea rubella, new genus, new species is described from Brazil (Mato Grosso). Neoderoploa willineri Kormilev, 1955 is placed as a junior synonym of $N$. bruchii Pennington, 1922. Diagnoses are given for the tribe Procleticini and for all previously described procleticine genera. Redescriptions are provided for several relatively rare species: Lobepomis peltifera Berg, Procleticus corniger Berg, Terania guachipasi Pirán, and Neoderoploa bruchii Pennington. A key to aid in the identification of the included genera is provided.


Pennington (1920) established the tribe Procleticini to hold two monotypic genera, Procleticus Berg and Lobepomis Berg. He characterized the tribe as having spined or lobed humeral angles, the scutellum large and nearly reaching the apex of the abdomen, the abdomen very convex below, and the rostrum not surpassing the hind coxae. In 1922, Pennington described Neoderoploa bruchii and stated that it was related to Lobepomis without mentioning the tribe Procleticini. Kormilev (1955) described a second species of Neoderoploa and formally placed the genus in the Procleticini. There has been no further mention of the tribe Procleticini since Pirán (1963) added his new genus, Terania, to the tribe.

I believe that the Procleticini are a valid tribe, but its definition should be broadened to include six more genera previously placed in the Pentatomini and one new genus: Aleixus McDonald, Brepholoxa Van Duzee, Dendrocoris Bergroth, Odmalea Bergroth, Parodmalea, new genus, Thoreyella Spinola, and Zorcadium Bergroth. Of Pennington's original defining characters only the convexivity of the abdomen and the length of the rostrum hold true for all eleven genera. There are, however, other characters, mainly those concerning the male and female genitalia, which bring these genera together as a homogeneous group. The Procleticini are restricted to the New World with most species neotropical in distribution.

Because most of the genera and species in this tribe have a small, anteriorlydirected, spine or tubercle at the base of the abdomen, they will key to section 2 of the Pentatomini in Rolston and McDonald's (1979) conspectus of higher taxa of Pentatomoidea. Parodmalea and males of several species of Dendrocoris lack the basal abdominal spine and will key to section 1 of the Pentatomini. These genera can be separated from Pentatomini by their characteristically shaped male and female
genitalia. The pygophoral inferior ridge of males is deeply incised medially and produced dorsad and/or cephalad laterally. The genital plates of females are small, subtriangular, and somewhat recessed into the last abdominal segment; the basal plates are usually very small and are often obscured under the caudal margin of the seventh abdominal sternite.

## Procleticini Pennington

Procleticini Pennington, 1920:7
Procletini [sic]: Kormilev, 1955:10; Pirán, 1963:338.
Diagnosis. Juga longer than tylus (except in some Odmalea concolor) and often contiguous in front of tylus. First antennal segment not reaching apex of head. Bucculae lobed posteriorly, each with anterior tooth; first rostral segment not surpassing posterior terminations of bucculae; rostrum usually not reaching beyond metacoxae. Each ostiolar ruga usually reaching middle of metapleuron, usually acuminate apically (except Brepholoxa). Thoracic sterna flat to sulcate. Third (second visible) abdominal sternite usually armed with anteriorly-directed spine (very small in Lobepomis and Procleticus, and lacking in Parodmalea and males of some Dendrocoris). Anterolateral pronotal margins straight to concave; humeral angles rounded to spinose, usually prominent, anterior pronotal angles dentate. Tarsi 3 -segmented.

Genital plates small and as group appearing recessed into venter; basal plates small and often partially or completely obscured by last abdominal sternite; second gonocoxae often emarginate distally; ninth paratergites subtriangular; sternite ten relatively large, quadrangular. Eighth paratergites lacking spiracles. Pygophore somewhat produced posteriorly with distinct medial emargination which may be either narrow and parallel sided or often becoming circular ventrally; usually with small emargination between lateral margins and superior ridge.

Comments. The included genera can be separated into two groups based primarily on the shape and length of the scutellum. In Lobepomis, Neoderoploa, Procleticus, and Terania, the scutellum is spatulate and nearly reaches the apex of the abdomen, completely obscuring the hemelytral membranes. In Aleixus, Brepholoxa, Dendrocoris, Odmalea, Parodmalea and Zorcadium the scutellum is subtriangular and does not reach beyond the apices of the coria. Thoreyella is intermediate in that the scutellum is not as triangular as in the latter group of genera, and although the scutellum does not approach the apex of the abdomen it is subequal to or slightly longer than the coria.

Other than the male and female genitalia, none of the above characters will define this tribe by themselves. Most genera, however, can be placed in this tribe by a combination of the above characters. The male and female genitalia seem to follow the same general shape within all genera studied and appear to be unique within the Pentatomidae.

## KEY TO THE GENERA OF THE TRIBE PROCLETICINI

1 Scutellum enlarged, extending distinctly beyond apices of coria to near apex of abdomen (Fig. 1)

- Scutellum not enlarged, usually not extending beyond apices of coria, not approaching apex of abdomen (Fig. 59)2(1) Superior surface of each tibia flattened, with distinct coarse punctures3
- Superior surface of each tibia rounded, flattened, or sulcate, but lacking punctures43(2) Scutellum with distinct black fovea in each basal angle; humeral angles broad,flattened, flaring dorsad, each bearing one sharp spine and three or more blunt teeth(Fig. 1)Lobepomis Berg
- Scutellum lacking black fovea; humeral angles large, robust, horn-like, each withsingle anterolaterally-directed, sharp spine (Fig. 17)Procleticus Berg
4(2) Pronotal disc lacking transverse, pale carinae (Fig. 31) Terania Pirán
- Pronotal disc with two transverse, pale carinae, one between humeral angles andone just posterior to pronotal cicatrices (Fig. 45) . . . . . . . . . . Neoderoploa Pennington5(1) Distal end of each ostiolar ruga rounded, unattached to metapleural plate, rugashort, reaching less than half the distance from mesial margin of ostiole to lateralmetapleural margin (Fig. 61) . . . . . . . . . . . . . . . . . . . . . . . . . . . . Brepholoxa Van Duzee- Distal end of each ostiolar ruga acuminate, attached to metapleural plate, ruga long,reaching more than half the distance from mesial margin ostiole to lateral meta-pleural margin (Fig. 80)6
6(5) Superior surface of each femur prolonged distally as small spine (Fig. 111) ..... 7
- Femora not so armed (Fig. 93) Dendrocoris Bergroth7(6) Third (second visible) abdominal sternite bearing anteriorly directed spine or tu-bercle8
- Abdomen unarmed ventrally Parodmalea, new genus
8(7) Juga contiguous before tylus (Fig. 137) ..... 10
- Juga usually separated apically (Fig. 117), if contiguous then coria decidedly bicol- ored, stramineous and castaneous ..... 9
9(8) Humeri bearing large dorsal tubercle (Fig. 116); second antennal segment longer than each succeeding segment . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Aleixus McDonald- Humeri not tuberculate (Fig. 121); second antennal segment shorter than each suc-ceeding segment . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Odmalea Bergroth10(8) Humeri cornute; costal angle of coria extending caudad well beyond apex of scu-tellum (Fig. 136) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Zorcadium Bergroth- Humeri angulate or spinose; costal angle of coria extending caudad little if anyfarther than apex of scutellum (Fig. 149)Thoreyella Spinola


## Lobepomis Berg

## Lobepomis Berg, 1891:236-237; Pennington, 1920:7.

Type species. Lobepomis peltifera Berg, 1891, by monotypy.
Diagnosis. Juga contiguous anteriorly; lateral margins sinuous (Fig. 2), not reflexed. Antenniferous tubercles visible in dorsal view. Antennal segments II and III subequal in length. Humeral angles broad, flattened, flaring dorsad, each bearing one sharp spine and three to five blunt teeth (Fig. 1). Scutellum broadly spatulate; apex broadly rounded, nearly reaching posterior margin of abdomen; distinct black fovea in each basal angle (Fig. 1). Anterior tooth of each buccula small, acute. Rostrum reaching between metacoxae. Each ostiolar ruga reaching middle of metapleuron. Thoracic sterna flat to broadly and weakly sulcate. Superior surface of each femur armed distally with small obtuse tooth; superior surface of each tibia flattened with distinct, coarse, darkened punctures. Basal abdominal spine very weak, sometimes obsolete.

Comments. Lobepomis is monotypic, containing only Lobepomis peltifera. This genus is probably most closely related to Procleticus, as both genera share the relatively






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Figs. 1-16. Lobepomis peltifera. 1. Habitus. 2. Head, dorsal view. 3-6. Pygophore. 3. Ventral view. 4. Dorsal view. 5. Caudal view. 6. Lateral view. 7-9. Theca. 7. Lateral view. 8. Ventral view. 9. Dorsal view. 10-14. Right paramere. 10. Caudal view. 11. Anterior view. 12. Lateral view. 13. Medial view. 14. Ectal view. 15. Spermatheca. 16. Genital plates, caudoventral view. Symbols: bp, basal plate; fv, fovea; gx2, second gonocoxa; jug, jugum; me, medial emargination in pygophore; par, paramere; pen, penisfilum; prt, proctiger; spb, spermathecal bulb; sr, sclerotized rod; sl0, sternite 10 ; tyl, tylus; 8 pt , eighth paratergite; 9 pt , ninth paratergite.
unique character of having the superior surfaces of the tibiae distinctly punctate. This species is redescribed to augment the original description.

Lobepomis peltifera Berg
Figs. 1-16
Lobepomis peltifera Berg, 1891:237-238.
Description. Small, ovate, brown to dark brown with fuscous to black punctures; punctures irregularly arranged leaving densely punctate areas intermixed with small, nearly impunctate areas.

Head brown, broadly rounded apically, with numerous fuscous punctures, distal third of head somewhat declivent when viewed laterally. Lateral jugal margins sinuous, slightly reflexed apically; juga usually contiguous anteriorly (Fig. 2); base of tylus elevated above juga. Vertex tumid with medial sulcus. Antennae dark brown, relatively short, segments II and III subequal in length and each only slightly shorter than segments IV or V, segments IV and V slightly thicker in diameter than first three segments.

Pronotum brown with fuscous punctures; anterior margin concave, elevated above surface; anterior disc with medial keel, becoming obsolete on posterior disc; cicatrices tuberculate, often with slightly angled carina between tubercle and median keel; sometimes second low tumescence located laterad of each cicatrical tubercle (Fig. 1). Anterolateral pronotal margins concave; humeral angles robust, flared dorsad, each possessing one dorsally-directed spine and 3-5 bluntly rounded to acute teeth. Posterior pronotal margin convex medially, angled posteriorly near basal angles of scutellum (Fig. 1). Distal width of scutellum slightly less than basal width (Fig. 1). Coria pale brown with fuscous punctures; each claval suture short, ending slightly beyond scutellar fovea; costal angle nearly reaching anterior margin of last connexival segment. Connexiva yellow-brown, densely black punctate except near transverse sutures.

Ventral surface yellow-brown, abdomen sometimes yellow-orange; punctures coarse, fuscous to black, rather sparsely and irregularly arranged. Ventral surface of head and thoracic pleura irregular with depressed and elevated areas. Ventral surface of head with black vitta on each side between antenna and anterior margin of buccula. Rostral segment II slightly longer than segment III or IV; rostrum reaching between metacoxae. Each ostiolar ruga reaching middle of metapleuron; evaporative areas black, reduced, just surrounding ostiolar rugae and one, angled, narrow streak on each mesopleuron. Legs yellow-brown, with dark brown punctures; tarsi dark brown. Spiracles pale, each on small, elevated callus. Ventral surface of abdomen impunctate medially, sparsely punctate laterally except dense ring of punctures around each spiracular callus and area of dense punctures near middle of each abdominal segment near lateral margins.

Basal plates relatively large, mesial margins nearly straight, posterior margins convex (Fig. 16). Ninth paratergites elongate, mesial margins angled, nearly straight; tenth sternite trapezoidal (Fig. 16). Spermatheca with sclerotized rod uniform in diameter throughout except narrowed and curved apically; spermathecal bulb digitiform, slightly bulbous basally (Fig. 15). Pygophore narrowed posteriorly with distinct depressed areas laterally and ventrally making caudal area appear produced


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Figs. 17-30. Procleticus corniger. 17. Habitus. 18. Head, dorsal view. 19-22. Pygophore. 19. Ventral view. 20. Dorsal view. 21. Caudal view. 22. Lateral view. 23-27. Left paramere. 23. Caudal view. 24. Anterior view. 25. Lateral view. 26. Medial view. 27. Ectal view. 28. Theca, lateral view. 29. Genital plates, caudoventral view. 30. Spermatheca.
posteriorly (Fig. 6); with distinct medial emargination easily visible in both caudal and ventral views (Figs. 3, 5); margins of emargination somewhat carinate dorsally, roundly obtuse and appearing to flare laterad ventrally. Proctiger relatively small, lateral and posterior margins not reflexed. Parameres relatively small, head of each
with two small lobes; shaft thickened in middle (Figs. 10-14). Aedeagus with penisfilum relatively large, robust, S-shaped (Fig. 7).

Types. Berg (1891) described this species from two specimens, one from Mendoza, Argentina, and the other from Uruguay. The types of this very distinctive species were not examined.

Specimens examined. 11 q, 5 か̂ô, 2 nymphs, collected from 16 November to March; deposited in AMNH, LILL, MLPA, USNM. ARGENTINA: Catamarca: Andalgalá; 6 km N Belén; El Rodeo; Pta. Balasto. Cordoba: Quilino; Rio Nono. Formosa: Formosa; Gran Guardia. Mendoza: Capitan Moyano; Mendoza to Cachueta. Salta: Salta. San Luis: Rt. 7, 23 mi SE San Luis City. Santiago del Estero: Jeaño.

Comments. This is the only species within the Procleticini with black foveae in the basal angles of the scutellum. It is one of two species having the superior surfaces of the tibiae distinctly punctate, the other being Procleticus corniger. These two species are easily separated by the lack of black foveae on the scutellum in $P$. corniger and by the differences in the shape of the humeral angles. The humeral angles of $L$. peltifera are broad, flattened, flaring dorsad with one sharp tooth and 3-5 blunt teeth; the humeral angles of $P$. corniger are horn-like, directed more anterolaterad, and lack blunt teeth.

The nymphs are of interest in that they have three thorn-like spines on the dorsal surface: one medially near the posterior margin of the pronotum and two on the scutellum, one in each basal angle. This may afford the individuals some protection from predation.

## Procleticus Berg

Procleticus Berg, 1891:234-235; Pennington, 1920:7.
Type species. Procleticus corniger Berg, 1891, by monotypy.
Diagnosis. Juga usually contiguous anteriorly; lateral margins sinuous (Fig. 18), not reflexed. Antenniferous tubercles visible from dorsal view. Antennal segments II and III subequal in length. Humeral angles spinose; anterolateral pronotal margins concave; disc of pronotum lacking transverse, pale carinae (Fig. 17). Scutellum spatulate, apex broadly rounded, nearly reaching apex of abdomen; basal angles lacking foveae; disc lacking pale, Y-shaped carina (Fig. 17). Anterior tooth of bucculae small, acute. Rostrum reaching between mesocoxae. Each ostiolar ruga reaching middle of metapleuron. Thoracic sterna sulcate. Superior surface of each femora armed distally with small acute tooth; superior surface of each tibia flattened, with distinct, coarse punctures. Basal abdominal spine very weak, sometimes obsolete.

Comments. Procleticus is monotypic containing only P. corniger. The species is redescribed to expand the original description.

## Procleticus corniger Berg

Figs. 17-30
Procleticus corniger Berg, 1891:235-236.
Description. Elongate oval, yellowish-brown with dark brown to fuscous punctures; punctures relatively sparsely but uniformly dispersed, becoming very dense near humeral angles.

Head light brown with fuscous punctures, base of tylus sometimes impunctate; apex broadly rounded; lateral jugal margins sinuous, not reflexed (Fig. 18). Dorsal surface of head flat apically, somewhat convex between eyes, becoming tumid on vertex; ocelli relatively widely spaced, lateral margin of each ocellus nearly even with mesial margin of adjacent compound eye. Antennae brown, segments II and III subequal in length, each only slightly shorter than either segment IV or V.

Pronotum light brown with dark brown punctures becoming denser and black near humeral angles; punctures arranged in indistinct lines consisting of 3-5 punctures at different angles; slightly elevated spaces between lines of punctures giving pronotum obscure, rugulose appearance. Anterior pronotal margin concave; anterolateral margins ecarinate, concave; humeral angles large, robust, each produced into anterolat-erally-directed horn-like, black spine (Fig. 17); posterior pronotal margin only weakly convex anterior to scutellum, slightly angled near basal angles of scutellum (Fig. 17). Distal width of scutellum slightly less than basal width (Fig. 17); punctures rather uniformly dispersed. Coria light brown with uniformly dispersed brown punctures; costal angle reaching to anterior margin of last connexival segment. Connexiva yel-low-brown with pale punctures becoming black along lateral margins of all segments and along posterior margin of last connexival segment.

Ventral surface yellow-brown, sometimes abdomen orange-brown, punctures pale brown to fuscous. Punctures on head black becoming more dense just anterior to antenniferous tubercles. Anterior tooth of each buccula small, acute, sometimes obscured by apically inflated juga. Rostral segments II, III, and IV subequal in length, each very short; rostrum reaching between mesocoxae. Thoracic pleura with relatively pale punctures becoming denser and darker laterally and around coxae. Each ostiolar ruga reaching middle of metapleuron, curving slightly cephalad apically; evaporative areas pale, reduced, just surrounding ostiolar rugae. Legs yellow-brown with numerous, small, dark brown punctures on superior surfaces of both femora and tibiae. Ventral surface of abdomen impunctate medially, rather densely punctate laterally, but punctures pale, concolorous with surface except for several fuscous punctures near posterolateral angle of last abdominal segment. Spiracles pale, only slightly elevated above abdominal surface, not on impunctate calli.

Basal plates small, subtriangular, only apices visible beyond margin of last abdominal segment (Fig. 29). Ninth paratergites subtriangular, posterior angles narrowly rounded; mesial margins slightly concave along 10th sternite, convex between 10th sternite and basal plates (Fig. 29). Spermatheca with sclerotized rod not curved but somewhat narrowed apically; spermathecal bulb robustly digitiform (Fig. 30). Pygophore in ventral view with medial emargination nearly circular, posteroventral surface concave laterally on each side, becoming obtusely prominent medially from medial emargination to small, obtuse, chin-like protuberance on posteroventral margin (Fig. 19); in caudal view, medial emargination relatively narrow, pygophoral rim just laterad of medial emargination broadly rounded, flaring upward and inward with smaller rounded emargination between it and posterolateral angles (Fig. 21); in dorsal view, inferior ridge black and roughened laterally with second ridge located just below inferior ridge laterally, large darkened tubercle on each anterolateral wall of genital cup which continues ventrally as slender sclerotized plate (Fig. 20). Paramere broad, thin basally, curving distinctly cephalad laterally; dorsomesial angle prolonged into long digitiform process directed dorsad and slightly laterad, apex curved slightly
caudad (Figs. 23-27). Aedeagus with penisfilum relatively large, robust, S-shaped (Fig. 28).

Types. Berg (1891) described this species from $1 \hat{\delta}$ and $1 \$$ specimen, both from Cordoba, Argentina. The types of this distinctive species were not examined.

Specimens examined. $10 \neq 9$, $3 \delta \hat{\delta}$, collected from 6 December to 17 June; deposited in AMNH, LILL, MLPA, USNM. ARGENTINA: Catamarca: Belén. Cordoba: Cordoba. Misiones: San Ignacio; Santo Pipo. Santiago del Estero: Lago Huyo; Rio Salado.

Comments. This species may be easily recognized by a combination of the following characters: broadly spatulate scutellum nearly reaching apex of abdomen, superior surfaces of tibiae distinctly punctate, scutellum lacking basal fovea, and humeral angles robust, horn-like.

## Terania Pirán

Terania Pirán, 1963:338.
Type species. Terania guachipasi Pirán, 1963, by original designation.
Diagnosis. Juga contiguous anteriorly; lateral margins not reflexed, weakly concave in middle; antenniferous tubercles slightly visible from dorsal view (Fig. 32). Antennal segment II shorter than segment III. Humeral angles flaring dorsad and laterad, ending in single darkened spine (Fig. 31). Anterolateral pronotal margins concave, with minute, vertical ridges; anterior and posterior pronotal margins obtusely carinate; pronotal disc lacking transverse carinae. Scutellum narrowly spatulate, apex broadly rounded, reaching to or slightly beyond apex of abdomen; basal angles lacking foveae; disc lacking pale Y-shaped carina. Anterior tooth of each buccula small, obtuse. Rostrum reaching onto base of abdomen. Each ostiolar ruga reaching slightly beyond middle of metapleuron, curving cephalad apically. Thoracic sterna broadly and shallowly concave. Superior surface of each femora armed distally with small acute tooth; superior surfaces of tibiae asulcate, flattened, impunctate. Basal abdominal spine small.

Comments. Terania is monotypic containing only T. guachipasi. This species is rare in collections and has not been mentioned since its original description in 1963. A redescription follows.

## Terania guachipasi Pirán

Figs. 31-44
Terania guachipasi Pirán, 1963:338-340, figs. 1, 2.
Description. Ovate, yellowish-brown with dark brown to fuscous punctures on pronotum, scutellum and hemelytra. Punctures small, relatively sparse, uniformly dispersed.

Head with punctures relatively dense, concolorous with surface; vertex distinctly convex, becoming slightly concave near apex of tylus; apex broadly rounded. Lateral jugal margins slightly concave in middle, not reflexed (Fig. 32). Antennal segment II about two-thirds length of segment III; segments IV and V slightly inflated and darker than first three segments. Pronotum with punctures dark brown to fuscous except pale anteriorly and laterally, those on posterior disc forming vague, rugulose



38




Figs. 31-44. Terania guachipasi. 31. Habitus. 32. Head, dorsal view. 33-36. Pygophore. 33. Ventral view. 34. Dorsal view. 35. Caudal view. 36. Lateral view. 37-41. Left paramere. 37. Caudal view. 38. Anterior view. 39. Lateral view. 40. Medial view. 41. Ectal view. 42. Theca, lateral view. 43. Genital plates, caudoventral view. 44. Spermatheca.
lines. Anterior pronotal margin strongly concave, obtusely carinate; anterolateral pronotal margins concave, obtusely carinate, minutely, vertically ridged; humeral angles flaring dorsad and laterad, each ending in small, darkened spine (Fig. 31); fuscous streak on posterolateral pronotal margin extending for short distance along
anterolateral margin near each humeral angle. Posterior pronotal margin uniformly convex throughout, obtusely carinate anterior to scutellum (Fig. 31); pronotal disc with pale, longitudinal, impunctate line medially. Scutellar punctures small, fairly uniformly dispersed, dark brown to fuscous, becoming pale near posterior margin; distal width of scutellum only slightly more than half basal width; lateral scutellar margins nearly parallel for posterior half, infuscated near inner basal angles of coria; scutellar disc with medial, longitudinal, pale, impunctate line becoming obscure anteriorly. Coria with punctures small, uniformly dispersed, dark brown; posterior margins slightly convex, matching contour of scutellum; costal angle rounded, reaching onto last connexival segment; hemelytral membranes translucent, veins only vaguely apparent. Connexiva uniform in color, punctures concolorous.

Punctures on ventral surface of head, thorax, and abdomen pale, shallow. Ventral surface of head with small fuscous vitta on each side between eye and antenniferous tubercle. Antenniferous tubercles obtusely rounded apically. Ventral surfaces of juga roundly lobed apically, covering apices of bucculae. Rostral segments II and III subequal in length, segment IV slightly shorter, reaching onto base of abdomen. Each ostiolar ruga distinctly curved cephalad apically, reaching slightly beyond middle of metapleuron. Legs pale, tarsi somewhat darker brown. Punctures on abdomen somewhat smaller and denser, especially laterally; spiracles pale, slightly raised above surface of abdomen.

Basal plates, subtriangular, posteromesial angles nearly acute; ninth paratergites broad, slightly concave along 10th sternite (Fig. 43). Sclerotized rod of spermatheca curved apically; spermathecal bulb robustly digitiform (Fig. 44). Pygophore with deep medial slit, easily visible in both ventral and caudal views (Figs. 33, 35), sides of emargination nearly parallel; posterolateral margins of genital cup produced entad over opening. Ventral surface of pygophore anterior to emargination narrowly flattened for short distance, ending near small, arcuate, posteriorly-directed carina; surface of pygophore on each side of emargination deeply concave. Parameres as in Figures 37-41. Penisfilum relative robust (Fig. 42).

Type. Pirán (1963) described this species from a single $\$$ from Guachipas Department of the Province of Salta in Argentina on 7 November 1959. The holotype, which was examined, is conserved in the Universidad Nacional de La Plata, Argentina.

Specimens examined. 1̊, 2ô̂ô, collected on 7 November and 16 January; deposited in LHR, MLPA. ARGENTINA: Corrientes. Salta: Guachipas.

Comments. This species has the same general appearance as species of Neoderoploa. It can be easily separated from species of that genus by the lack of pale carinae on the dorsal surfaces of the pronotum and scutellum and by each humeral angle terminating in a single spine. Species of Neoderoploa have several pale carinae on the dorsal surface of the pronotum, a Y-shaped carina on the scutellum, and each humeral angle terminates in two or more spines.

## Neoderoploa Pennington

Neoderoploa Pennington, 1922:317-318; Kormilev, 1955:10.
Type species. Neoderoploa bruchii Pennington, 1922, by monotypy.
Diagnosis. Juga nearly contiguous anteriorly; lateral margins sinuous (Fig. 46), not
reflexed. Antenniferous tubercles visible from dorsal view. Antennal segment II shorter than segment III. Humeral angles bispinose, each produced beyond base of adjacent corium; anterolateral pronotal margins angulate near middle; pronotal disc with three transverse, pale carinae (Fig. 45). Scutellum narrowly spatulate, apex broadly rounded, nearly reaching apex of abdomen; basal angles lacking foveae; disc with Y-shaped, pale carina (Fig. 45). Rostrum reaching to anterior margins of metacoxae. Each ostiolar ruga acuminate apically, reaching beyond middle of metapleuron. Thoracic sterna flat to broadly and weakly sulcate. Femora each armed with small obtuse tooth distally; superior surfaces of tibiae asulcate, flattened, impunctate. Basal abdominal spine small.

Comments. At present Neoderoploa contains only N. bruchii Pennington, 1922; N. willineri Kormilev, 1955 is a junior synonym.

## Neoderoploa bruchii Pennington

Figs. 45-58
Neoderoploa bruchii Pennington, 1922:318, fig. 2; Kormilev, 1955:11.
Neoderoploa willineri Kormilev, 1955:10-12, figs. 3, 4. NEW SYNONYMY.
Description. Ovate, yellow to yellow brown with green tinting (probably mostly green when alive); punctures pale brown to brown.

Head yellow; punctures concolorous; vertex and base of tylus tumid; base of juga flatly angled toward eyes; distal one-third of head concave. Lateral margins of juga sinuous, not reflexed; apex of head rounded (Fig. 46). Antennae yellow to yellowgreen; segment II shorter than segment III; segments IV and V slightly inflated. Pronotum yellow with concolorous or pale brown punctures becoming darker near humeral angles; punctation dense, coarse, somewhat reticulate between pronotal carinae. Anterior pronotal margin broadly and shallowly V-shaped, obtusely carinate, pale, extended over base of head nearly to posterior margins of ocelli (Fig. 46). Pronotum with transverse, pale, roughened callus or carina just posterior to pronotal cicatrices; another transverse, pale, well-defined carina between humeral angles; with medial, longitudinal, pale line or carina (Fig. 45); surface between pronotal calli slightly inflated. Anterolateral pronotal margins angulately concave, somewhat obtusely carinate, slightly roughened; humeral angles broadly flaring laterad and dorsad, each with single very strong spine and single obtuse tooth anterior to spine (Fig. 45); humeral spine red. Posterolateral pronotal margins roughened, with thin, slightly curved, black line from humeral angle to base of each corium; posterior pronotal margin broadly convex, obtusely carinate, not angulate near basal angles of scutellum (Fig. 45). Distal width of scutellum slightly more than half basal width; with pale, longitudinal carina running from apex to level of frena, then bifurcating to near basal angles (Fig. 45); lateral scutellar margins carinate along frena; apex of scutellum rounded with small medial indentation; scutellar punctation dense and strong near Y-shaped carina, becoming sparse and weak laterally and apically. Coria somewhat weakly punctate; $\mathrm{R}+\mathrm{M}$ vein somewhat elevated, inner margin impunctate; costal angle nearly reaching anterior margin of last connexival segment. Connexiva yellow, immaculate.

Ventral surface of head yellow; punctures concolorous except sometimes with several reddish punctures near base; with black vitta between eyes and antenniferous


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Figs. 45-58. Neoderoploa bruchii. 45. Habitus. 46. Head, dorsal view. 47-50. Pygophore. 47. Ventral view. 48. Dorsal view. 49. Caudal view. 50. Lateral view. 51-55. Right paramere. 51. Lateral view. 52. Medial view. 53. Anterior view. 54. Caudal view. 55. Ectal view. 56. Theca, lateral view. 57. Genital plates, caudoventral view. 58. Spermatheca.
tubercles; eyes and antenniferous tubercles not contiguous. Rostral segment II longer than either III or IV, segment IV reaching between mesocoxae. Each thoracic pleura with diagonal, pale, impunctate area on each side, those on propleura and mesopleura originating near coxal clefts and running anterolaterad, those on metapleura also
running anterolaterad just posterior to evaporative areas. Each ostiolar ruga strongly elevated, curved cephalad apically, reaching about two-thirds distance to lateral metapleural margin. Legs yellow to pale brown, sometimes tibiofemoral joints reddish. Ventral surface of abdomen pale yellow, with numerous, small, concolorous punctures. Spiracles pale, each located on elevated, yellow callus. Basal abdominal spine relatively stout, reaching to anterior margins of metacoxae.

Basal plates small, partially obscured by ventral margin of last abdominal segment, somewhat vertical, posterior margin rounded; ninth paratergites subtriangular, mesial margins concave, posterior angles rounded; tenth sternite trapezoidal (Fig. 57). Spermatheca with sclerotized rod nearly uniform in width; spermathecal bulb digitiform (Fig. 58). Medial emargination of pygophore visible in ventral view (Fig. 47), nearly circular in caudal view (Fig. 49), in dorsal view sides of emargination convex, nearly contiguous medially (Fig. 48), posterior wall of genital cup with irregular black ridges and teeth (Fig. 48). Posterior surface of pygophore strongly produced caudad around medial emargination (Figs. 49, 50), concave laterally. Parameres bilobed (Figs. 5155); penisfilum moderate in form (Fig. 56).

Types. Pennington (1922) described this species from Cordoba, Argentina. The type specimen of $N$. willineri Kormilev was examined, and although there are some subtle differences in the shape of the humeral angles, I believe these differences to be minor and place $N$. willineri as a junior synonym of $N$. bruchii. The holotype of $N$. willineri is conserved in the Instituto de Investigaciones Entomologicas Salta, Argentina.

Specimens examined. 5 와, 1 î collected from 15 November to 16 February; deposited in AMNH, FSCA, MLPA. ARGENTINA: Cordoba: 5 mi N Dean Funes; Huerta Grande. Salta: Pocitos. BOLIVIA: Cochabamba: Cochabamba.

Comments. This is a very striking species and is easily identified by the transverse carinae on the pronotum and the strong Y-shaped carina on the scutellum.

## Brepholoxa Van Duzee

Figs. 59-77
Brepholoxa Van Duzee, 1904:78; Bergroth, 1908:178; Kirkaldy, 1909:150; Van Duzee, 1909:384; Van Duzee, 1917:65; Barber, 1939:286; Rolston, 1978:20; Rolston \& McDonald, 1981:259; Froeschner, 1988:567.

Type species. Brepholoxa heidemanni Van Duzee, 1904, by monotypy.
Diagnosis. Juga usually contiguous before tylus; lateral margins slightly to moderately sinuous, not reflexed (Fig. 60). Antenniferous tubercles visible in dorsal view. Antennal segment II longer than each remaining segment. Anterolateral pronotal margins straight to concave, armed with several small teeth anteriorly; humeral angles narrowly rounded to acute, often prominent (Fig. 59). Scutellum triangular, apex narrowly rounded, nearly acute; coria distinctly longer than scutellum (Fig. 59). Rostrum reaching hind coxae. Thoracic sterna distinctly sulcate. Each ostiolar ruga auriculate, apex narrowly rounded, not attached to metapleuron, not reaching middle of metapleuron (Fig. 61). Femora unarmed distally (Fig. 75); superior surfaces of tibiae asulcate, rounded, impunctate. Spiracles not located on calli. Basal abdominal spine reaching between metacoxae.

Comments. Within the Procleticini the genus Brepholoxa can be recognized by the


Figs. 59-77. Brepholoxa heidemanni. 59. Habitus. 60. Head, dorsal view. 61. Metapleuron. 62. Head, lateral view. 63-66. Pygophore. 63. Ventral view. 64. Dorsal view. 65. Caudal view. 66. Lateral view. 67-69. Theca. 67. Ventral view. 68. Lateral view. 69. Dorsal view. 70-74. Right paramere. 70. Lateral view. 71. Ectal view. 72. Medial view. 73. Anterior view. 74. Caudal view. 75. Femur. 76. Spermatheca. 77. Genital plates, caudoventral view. Symbols: af, apex of femur; buc, buccula; ea, evaporative area; or, ostiolar ruga.
triangular shaped scutellum and the short, auriculate ostiolar rugae. At present, Brepholoxa contains only two named species, B. heidemanni and B. rotundifrons Barber. There are, however, several undescribed species from Mexico and the West Indies which will be described in revision of the genus already in progress. All known species occur in the West Indies or bordering areas (Florida, Yucatan Peninsula).

## Dendrocoris Bergroth

Figs. 78-95
Liotropis Uhler, 1877:399-400; Uhler, 1886:5; Lethierry \& Severin, 1893:186; Van Duzee, 1904:62. [preoccupied]
Dendrocoris Bergroth, 1891:228; Summers, 1898:41; Barber, 1906:262-263; Bergroth, 1908:177; Kirkaldy, 1909:151; Banks, 1910:84; Barber, 1911:268; Kirkaldy, 1912:126; Bergroth, 1914:438, 439; Parshley, 1915:173; Van Duzee, 1917:64; Stoner, 1920:113; Parshley, 1923:759, 769; Blatchley, 1926:173; Torre-Bueno, 1939:241; Froeschner, 1941:128; Nelson, 1955:49-53; Rolston, 1978:21; Rolston \& McDonald, 1981:259; Froeschner, 1988:575. [new name]
Atizies Distant, 1893:456; Lethierry \& Severin, 1893:267; Kirkaldy, 1909:67. [syn. by Nelson, 1955]

Type species. Liotropis humeralis Uhler, 1877, by monotypy.
Diagnosis. Juga usually contiguous anteriorly; lateral margins usually sinuous, not reflexed (Fig. 79). Antenniferous tubercles slightly visible in dorsal view (Fig. 79). Antennal segment II equal to or shorter than segment III, sometimes shorter than segment I. Humeral angles rounded to spinose, each usually produced slightly beyond base of adjacent corium; anterolateral pronotal margins straight to concave (Fig. 78). Scutellum subtriangular; apex rounded to broadly rounded, not reaching beyond apices of coria (Fig. 78). Rostrum reaching anterior margins of metacoxae. Each ostiolar ruga acuminate apically, reaching beyond middle of metapleuron (Fig. 80). Thoracic sterna flat to slightly sulcate. Femora unarmed distally (Fig. 93); superior surfaces of tibiae sulcate. Basal abdominal spine small, lacking in males of some species.

Comments. Within the Procleticini, Dendrocoris can be recognized by the following combination of characters: subtriangular scutellum which does not reach the corial apices, ostiolar rugae elongate and acuminate apically, and the femora are unarmed distally. Dendrocoris appears to be most closely related to Odmalea and Thoreyella but can be separated from both of those genera by the unarmed femora.

Nelson (1955) revised Dendrocoris providing descriptions of and a key to all known species. He later added another species to the genus (Nelson 1957). Thomas (1984) added a species from Mexico and provided a key to those species of Dendrocoris known to occur in Mexico. At present, Dendrocoris contains eleven species: D. arizonensis Barber, 1911, D. contaminatus Uhler, 1897, D. fruticicola Bergroth, 1891, D. humeralis (Uhler, 1877), D. maculosus Thomas, 1984, D. neomexicanus Nelson, 1955, D. parapini Nelson, 1957, D. pini Montandon, 1893, D. reticulatus Barber, 1911, D. suffultus (Distant, 1893), and D. variegatus Nelson, 1955. I have examined specimens of all species except $D$. maculosus. Many species of Dendrocoris occur in North America with several reaching southward into Mexico and Central America.


Figs. 78-95. Dendrocoris humeralis. 78. Habitus. 79. Head, dorsal view. 80. Metapleuron. 81-84. Pygophore. 81. Ventral view. 82. Dorsal view. 83. Caudal view. 84. Lateral view. 8587. Theca. 85. Lateral view. 86. Ventral view. 87. Dorsal view. 88-92. Right paramere. 88. Caudal view. 89. Anterior view. 90. Lateral view. 91. Medial view. 92. Ectal view. 93. Femur. 94. Spermatheca. 95. Genital plates, caudoventral view.

## Parodmalea, new genus

Type species. Parodmalea rubella, new species.
Description. Juga usually narrowly rounded apically, slightly longer than tylus but not contiguous anteriorly; lateral margins sinuous, often slanted slightly dorsad, slightly reflexed (Fig. 97). Antenniferous tubercles visible from dorsal view. Surface of head usually slightly depressed between eyes. Antennal segment II less than half length of segment III. Humeral angles spinose; anterolateral pronotal margins concave in dorsal view (Fig. 96), usually with several small denticles. Pronotal disc brown to reddish brown with fuscous punctures, with small fuscous spot on each side of midline and sometimes second spot on each side equidistant from first spot and lateral pronotal margin. Scutellum subtriangular, brown with small, fuscous spot along each lateral margin near distal end of frenum; apex rounded, not reaching corial apices (Fig. 96). Each corium brown to reddish brown with large, pale, impunctate spot on basal third and usually with small, pale, impunctate area near apex. Hemelytral membranes transparent, sometimes infuscated near mesial basal angle; veins subparallel.
Ventral surface pale yellow except punctures on head and broad lateral margin of propleura fuscous, fuscous sometimes spilling onto surfaces between punctures and often onto anterolateral angles of mesopleura. Thoracic sterna flat. Rostrum reaching between metacoxae. Each ostiolar ruga curving slightly cephalad, reaching about three-fourths distance to lateral metapleural margin. Superior surface of each femur bearing small acute tooth distally (Fig. 111); superior surfaces of tibiae asulcate, rounded, impunctate. Base of abdomen unarmed.

Comments. This genus at present contains a single species, $P$. rubella, herein described. I have single male specimens of four more undescribed species and two unattached female specimens. I have decided to refrain from describing these remaining species until more specimens are available. This genus appears to be restricted to South America.

This genus is closely related to the genus Odmalea. The typical color pattern in species of Parodmalea is nearly identical to that of several species of Odmalea. Species of Parodmalea lack the basal abdominal spine that is characteristic of species of Odmalea. Also, most species of Odmalea have the apices of the juga more broadly rounded than in species of Parodmalea.

Etymology. This genus is named for its resemblance to, and apparently close relatedness to, the genus Odmalea.

## Parodmalea rubella, new species

Figs. 96-114
Description. Small, ovate, reddish-brown with dark brown to fuscous punctures.
Head subtriangular; light brown basally becoming red apically; punctures deep, coarse, relatively dense, dark brown; small impunctate area on each side near inner basal angle of each eye. Lateral jugal margins sinuous near eyes, but nearly straight apically; apices of juga narrowly rounded, nearly acute (Fig. 97). Antenniferous tubercles clearly visible in dorsal view (Fig. 97). Surface of head slightly tumid between ocelli, relatively flat between eyes, lateral jugal margins elevated above surfaces of juga; apical half of juga declivent in lateral view. Antennae pale yellowish-brown,



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Figs. 96-114. Parodmalea rubella. 96. Habitus. 97, 98. Head. 97. Dorsal view. 98. Lateral view. 99-102. Pygophore. 99. Ventral view. 100. Dorsal view. 101. Caudal view. 102. Lateral view. 103-105. Theca. 103. Lateral view. 104. Ventral view. 105. Dorsal view. 106-110. Right paramere. 106. Lateral view. 107. Medial view. 108. Caudal view. 109. Anterior view. 110. Ectal view. 111. Femur. 112. Metapleuron. 113. Spermatheca. 114. Genital plates, caudoventral view.
segments I-II sometimes reddish, segments IV-V slightly thickened and sometimes darker brown; segment II less than half the length of segment III.

Pronotum dark brown around calli, becoming light brown posteriorly and along anterior margin, with thin, longitudinal, pale, impunctate line medially; humeral angles reddish; punctures coarse, dense, dark brown to fuscous, becoming reddish
near humeral angles. Anterior margin of pronotum deeply concave; anterolateral margins concave, not carinate, provided with series of small, widely spaced denticles, those on half nearest humeral angles distinctly larger than those on anterior half. Humeral angles sharply spinose, directed laterad (Fig. 96). Posterior pronotal margin slightly convex near scutellar margin. Scutellum light brown becoming reddish apically, with large, basal, fuscous spot medially (Fig. 96); punctures dark brown to fuscous. Coria light reddish brown, each with large, pale, reddish-yellow, impunctate spot near base (Fig. 96); impunctate spot including basal third of endocorium except for two rows of punctures along claval suture; punctures dark brown becoming reddish apically, with dense row of punctures along outer margin of $R+M$ vein; narrow, longitudinal, impunctate area long outer margin of $R+M$ vein. Hemelytral membranes translucent, lacking brown markings. Connexiva immaculate, pale yellow, sometimes tinged with red; posterolateral angle of last connexival segment produced posteriorly, spinose.

Ventral surface of head dark reddish-brown; punctures dark brown. Antenniferous tubercles nearly contiguous with eyes. Rostral segment IV slightly shorter than III, segment II longest, segment IV black apically, reaching between metacoxae. Ventral surfaces of thoracic segments pale yellow except lateral three-fourth of propleura and anterior margin of mesopleura dark reddish-brown, becoming red near humeral angles; punctures concolorous. Each ostiolar ruga nearly straight, reaching about three-fourths distance to lateral metapleural margin; evaporative areas relatively large (Fig. 112). Legs pale yellow; superior surface of each femur armed distally with small acute tooth (Fig. 111); superior surfaces of protibiae and mesotibiae asulcate, rounded; superior surfaces of metatibiae flattened, each sometimes with vague sulcation. Venter impunctate, shiny, pale yellowish-brown, becoming reddish near lateral and posterior margins. Spiracles pale.

Basal plates very small, obscured under posterior margin of last abdominal segment; posterior angles rounded. Ninth paratergites large, mesial margins nearly straight, divergent, posterior and lateral margins roundly convex; sternite 10 trapezoidal (Fig. 114). Spermatheca with sclerotized rod uniform in width except narrowed apically; spermathecal bulb short, cone-shaped (Fig. 113). Pygophore with broad medial emargination easily visible in both caudal and ventral views; margins of emargination divergent dorsally (Figs. 99, 101). Dorsolateral pygophoral margin moderately incised, posterolateral angles in lateral view lunate (Fig. 102), in caudal view apex rounded mesially, angulate laterally, not bilobate (Fig. 101). Proctiger not occupying most of genital capsule; its lateral and posterior margins distinctly reflexed (Fig. 101). Superior ridge not noticeably produced medially (Fig. 100). Parameres relatively large, each with relatively narrow shaft; head of each paramere bilobed, one horizontal, one vertical; vertical lobe narrowly rounded apically with small spinose tooth at anterodorsal angle; horizontal lobe broadly rounded apically (Figs. 106-110).

Measurements (mm). Total length 5.89-6.76 (6.28); total width 5.64-6.24 (5.67); medial length of pronotum 1.32-1.49 (1.47). Medial length of scutellum 2.72-3.16 (2.87); basal width 2.81-3.24 (2.87); width at distal end of frena 1.25-1.44 (1.33). Length of head 1.28-1.40 (1.29); width across eyes 1.81-2.08 (1.94); interocellar distance $0.55-0.64$ ( 0.57 ); interocular distance $1.00-1.12$ (1.05); ocellar diameter $0.12-0.15(0.12)$; distance from ocellus to adjacent eye $0.18-0.19$ ( 0.18 ). Length of segments I-V of antennae $0.33-0.37$ (0.33), $0.24-0.48$ ( 0.24 ), 1.07-1.14 (1.14), 0.94


Figs. 115-120. Aleixus virgatus. 115. Habitus. 116. Head and pronotum, anterior view. 117. Head, dorsal view. 118. Femur. 119. Metapleuron. 120. Genital plates, caudoventral view.
(0.94), and 0.96 (0.96), respectively. Length of segments II-IV of rostrum 0.75-0.88 ( 0.88 ), 0.61-0.77 (0.68), and 0.55-0.61 (0.61), respectively.

Holotype. ${ }^{\circ}$, labeled "BRAZIL, Mato Grosso: $12^{\circ} 31^{\prime}$ N: $55^{\circ} 37^{\prime}$ W Sinop, Oct. 1975 M. Alvarenga." Deposited in American Museum of Natural History, New York.

Paratypes. 4와 1ô. $3 \neq \mp$ 1ồ labeled "BRAZIL, Mato Grosso: Sinop, October 1976 M. Alvarenga" ( $2 \neq 9$ AMNH, $1 \circ$ 1九 DAR); and 19 labeled "BRAZIL, Mato Grosso: Vila Vera, $55^{\circ} 30^{\prime}$ long., $12^{\circ} 46^{\prime}$ lat., Oct. 1973 M. Alvarenga" (AMNH).

Distribution. Brazil (Espiritu Santo and Mato Grosso).
Comments. This is a very distinctive species, and can be recognized by a combination of the following characters: the large fuscous spot on the scutellar base, the reddish cast of the dorsum, the completely transparent hemelytral membranes, the denticulate anterolateral pronotal margins, and antennal segment II less than onehalf the length of segment III.

Etymology. This species is named rubella in reference to the distinct reddish cast of the dorsum.

## Aleixus McDonald

Figs. 115-120
Aleixus McDonald, in Rolston \& McDonald, 1981:259, 260.
Types species. Aleixus virgatus McDonald, 1981, by original designation.
Diagnosis. Juga surpassing tylus, but not contiguous anteriorly; lateral jugal margins distinctly sinuous, slightly reflexed (Fig. 117); apex of head distinctly declivent when


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Figs. 121-135. Odmalea concolor. 121. Habitus. 122. Head, dorsal view. 123. Metapleuron. 124-127. Pygophore. 124. Ventral view. 125. Dorsal view. 126. Caudal view. 127. Lateral view. 128-132. Right paramere. 128. Caudal view. 129. Anterior view. 130. Lateral view. 131. Medial view. 132. Ectal view. 133. Femur. 134. Genital plates, caudoventral view. 135. Spermatheca.
viewed laterally. Antenniferous tubercles clearly visible in dorsal view. Antennal segment II longer than each of remaining segments, segments II and III cylindrical, segments IV and V somewhat inflated. Humeral angles each bearing large tubercle, in anterior view obtusely rounded dorsally with two lateral projections, one obtuse and one nearly spinose (Fig. 116). Scutellum subtriangular, apex broadly rounded, not reaching apices of coria (Fig. 115). Rostrum reaching metacoxae. Each ostiolar ruga acuminate apically, reaching beyond middle of metapleuron (Fig. 119). Thoracic

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Figs. 149-167. Thoreyella brasiliensis. 149. Habitus. 150. Head, dorsal view. 151. Metapleuron. 152-155. Pygophore. 152. Ventral view. 153. Dorsal view. 154. Caudal view. 155. Lateral view. 156-158. Theca. 156. Lateral view. 157. Ventral view. 158. Dorsal view. 159-
from the single female holotype from Manaus, Brazil. The holotype of $A$. virgatus, which is conserved in the U.S. National Museum of Natural History, was examined.

Odmalea Bergroth

Figs. 121-135
Odmalea Bergroth, 1914:436-437; Rolston, 1978:20-23; Rolston \& McDonald, 1981: 259; Froeschner, 1988:588.

Type species. Odmalea quadripunctula Bergroth, 1914 [=Mormidea concolor Walker, 1867], by original designation.

Diagnosis. Juga usually longer than tylus (juga and tylus subequal in length in $O$. concolor), but usually not contiguous anteriorly; lateral jugal margins sinuous (Fig. 122). Antennal segment II shorter than segment III. Humeral angles rounded to spinose; anterolateral pronotal margins concave (Fig. 121). Scutellum subtriangular, not reaching beyond apices of coria; apex rounded (Fig. 121). Rostrum reaching to at least anterior margins of metacoxae. Each ostiolar ruga acuminate apically, reaching beyond middle of metapleuron (Fig. 123). Thoracic sterna flat. Superior surface of each femur armed distally with small spine (Fig. 133); superior surfaces of tibiae flattened to sulcate, impunctate. Basal abdominal spine small.

Comments. Odmalea is most closely related to Dendrocoris and Thoreyella. Odmalea can be separated from Dendrocoris by the distal spine on the femora; they are unarmed in Dendrocoris. A couple of characters are useful in separating species of Odmalea and Thoreyella. In Odmalea, the juga are not contiguous anteriorly and the scutellum is subtriangular, not reaching the apices of the coria. In Thoreyella, the juga are usually contiguous anteriorly and the scutellum is somewhat intermediate in shape, but usually reaches to or slightly beyond the apices of the coria.

At present, Odmalea contains six species: O. basalis (Walker, 1867), O. concolor (Walker, 1867), O. norda Rolston, 1978, O. pallida (Jensen-Haarup, 1931), O. schaefferi (Barber, 1906), and O. vega Rolston, 1978. Rolston (1978) revised the genus, providing descriptions of and keys to all known species. I have examined specimens of all known species. All known species are restricted to Central or South America.

## Zorcadium Bergroth

Figs. 136-148
Zorcadium Bergroth, 1918:307-308; Rolston \& McDonald, 1981:259, 269.
Type species. Euschistus truncatus Fallou, 1888, by monotypy.
Diagnosis. Juga not contiguous anteriorly; lateral jugal margins sinuous (Fig. 137). Antennal segment II shorter than segment III. Humeral angles cornute; anterolateral pronotal margins concave (Fig. 136). Scutellum subtriangular, not reaching beyond
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163. Right paramere. 159. Caudal view. 160. Anterior view. 161. Lateral view. 162. Medial view. 163. Ectal view. 164. Head, lateral view. 165. Femur. 166. Spermatheca. 167. Genital plates, caudoventral view.
apices of coria; apex narrowly rounded (Fig. 136). Rostrum reaching between mesocoxae. Each ostiolar ruga acuminate apically, reaching beyond middle of metapleuron (Fig. 139). Thoracic sterna flat to weakly sulcate. Superior surface of each femur armed distally with small tooth (Fig. 138); superior surfaces of tibiae weakly sulcate. Basal abdominal spine small.

Comments. Zorcadium is monotypic containing only Z. truncatum which is easily identified by its cornute humeral angles. Rolston and McDonald (1981) recently gave a detailed description of both Zorcadium and its only included species, Z. truncatum.

Specimens examined. 2 $\hat{\delta} \hat{\text { a }}$, 19, collected 17-22 March and 10 August; deposited in ENGL, USNM, UZMH. BRAZIL. PERU: Satipo. ARGENTINA: Mato Grosso: $10^{\circ} 25^{\prime} \mathrm{S}, 59^{\circ} 28^{\prime} \mathrm{W}$.

## Thoreyella Spinola

Figs. 149-167
Thoreyella Spinola, 1850:79-80; Spinola, 1852:119-120; Stål, 1872:45; Lethierry \& Severin, 1893:176; Kirkaldy, 1909:137; Jensen-Haarup, 1931:319-320; Pirán, 1957: 67-68; Rolston, 1978:20, 21; Rolston \& McDonald, 1981:259; Rolston, 1984:826828.

Uditta Stål, 1860:23-24; Stål, 1867:531. [syn. by Stål, 1872]
Type species. Thoreyella brasiliensis Spinola, 1850, by monotypy.
Diagnosis. Juga usually contiguous anteriorly (often not contiguous in T. trinotata); lateral jugal margins sinuous (Fig. 150). Antennal segments II and III subequal in length. Humeral angles rounded to spinose; anterolateral pronotal margins concave (Fig. 149). Scutellum somewhat spatulate, reaching to or slightly beyond apices of coria, but not approaching apex of abdomen; apex broadly rounded; each basal angle lacking fovea (Fig. 149). Rostrum reaching between mesocoxae. Each ostiolar ruga acuminate apically, reaching beyond middle of metapleuron (Fig. 151). Thoracic sterna flat. Superior surface of each femur armed distally with small tooth (Fig. 165); superior surfaces of tibiae flattened to weakly sulcate. Basal abdominal spine small.

Comments. Thoreyella is closely related to Dendrocoris and Odmalea. Thoreyella has the superior surfaces of the femora armed distally; they are unarmed in Dendrocoris. In Thoreyella, the juga are usually contiguous anteriorly and the apex of the scutellum reaches to or beyond the corial apices. In Odmalea, the juga are usually not contiguous and the apex of the scutellum does not reach the apices of the coria.

Thoreyella contains 4 species: T. brasiliensis Spinola, 1850, T. cornuta Berg, 1883, T. taurus Jensen-Haarup, 1931, and T. trinotata Berg, 1878. Rolston (1984) revised Thoreyella, providing descriptions of and a key to all known species. I have examined specimens of all known species. All known species are distributed in South America.

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LHR - L. H. Rolston personal collection, Louisiana State University, Baton Rouge.

LILL—Fundación e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina, M. V. A. Toledo.

MLPA-Facultad de Ciencias Naturales y Museo, La Plata, Argentina, R. A. Ronderos.
USNM - United States National Museum of Natural History, Washington, D.C., T. J. Henry.
UZMN-Zoological Museum, University of Helsinki, Finland, A. Jansson.
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# WEST INDIAN COCCINELLIDAE V (COLEOPTERA): A REVIEW OF COCCIDULINI AND ADDITIONS TO PSOROLYMA SICARD 

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#### Abstract

The West Indian taxa of Coccidulini are reviewed, and a key to the genera is given. Two new species of Psorolyma Sicard, Psorolyma doyeni, n. sp., and Psorolyma baorucensis, n . sp., are described, a revised key to species is presented, and pertinent morphological structures are illustrated


The tribe Coccidulini is represented in the New World by very few genera, some of which have not previously been formally assigned to a subfamily or tribe. Psorolyma Sicard, Botynella Weise, Geodimmockius Chapin, and Bura Mulsant are here considered to be members of the Coccidulini. They are restricted to the West Indies and are the only native West Indian cocciduline genera known. In addition to these native genera, the ubiquitous Rhyzobius lophanthae (Blaisdell) is perhaps present although no West Indian specimens have been examined. This species was introduced from Australia into California more than 100 years ago and has since been introduced into many parts of the world. It is known to occur in North America (Gordon, 1985), Bermuda (Gordon and Hilburn, 1990), and South America (Gordon, in press) and therefore included in the following key. The South American taxa of the subfamily Coccidulinae are treated and the subfamily formally described by Gordon (in press).

## KEY TO WEST INDIAN GENERA OF COCCIDULINI

1. Dorsum densely pubescent with mixture of erect and decumbent hairs; postcoxal line complete

Rhyzobius Stephens
Dorsum feebly pubescent with scattered, erect hairs; postcoxal line incomplete2

2(1). Genal projection of clypeus broadly extended onto inner $1 / 3$ of eye (Fig. 14); clypeal apex truncate, not transparent; antenna not reaching posterior pronotal angle; body nearly round; dorsum entirely black with brassy sheen; Hispaniola ...... Bura Mulsant Clypeus without lateral projection; clypeal apex emarginate, or if truncate, then apex transparent; antenna reaching posterior pronotal angle or beyond; body elongate, or with outline of pronotum and elytron strongly discontinuous; dorsum variable in color; Hispaniola and elsewhere
3(2). Body color very dark (except Psorolyma sicardi pale with black spots); pronotum, elytron without reflexed, transparent margins; not known from Cuba (Fig. 17)

Psorolyma Sicard
Body color pale, often with dark spots on elytron; pronotum and elytron with reflexed, transparent margins; known only from Cuba
4(3). Outline of pronotum, elytron strongly discontinuous; eye very convex, "bugeyed"; clypeal apex transparent; lateral margins of pronotum and elytron extremely strongly reflexed (Fig. 15)

Geodimmockius Chapin

Outline of pronotum, elytron nearly continuous; eye somewhat convex; clypeal apex not transparent; lateral margins of pronotum and elytron moderately reflexed (Fig. 16)

Botynella Weise

## TAXA OF NATIVE WEST INDIAN COCCIDULINI

Bura Mulsant
Bura Mulsant, 1850:374, 419. Type species: Bura cuprea Mulsant, by monotypy.
Bura is a monobasic genus known only from Hispaniola and doubtfully from Cuba. It differs significantly from all other West Indian coccidulines in having a short, wide labium as in Figure 2 (Fig. 1 illustrates a characteristic cocciduline labium) and a strong lateral projection expanded onto the eye (Fig. 14). In addition, the apical maxillary palpal segment (not illustrated) is only slightly securiform, resembling that of some genera of Sticholotidini. The long, slender, 10 -segmented antenna with 3-segmented fusiform club (Fig. 3), protuberant prosternal projection (Fig. 6), absence of tibial spurs, tarsal claw toothed at base, and incomplete postcoxal line parallel to base of sternum, and 6 -segmented abdomen are characters shared with all other West Indian genera of Coccidulini, therefore Bura is considered correctly placed in this tribe.

Dimmock (1906) mentioned a single specimen from Cuba that he tentatively assigned to Bura. That specimen may not have been a species of Bura and the presence of the genus on Cuba is considered extremely doubtful.

## Botynella Weise

Botynella Weise, 1891:286. Type species: Botynella quinquepunctata Weise, by subsequent designation of Korschefsky, 1931.
Botynella quadripunctata Weise, 1891:287. Distribution: Cuba. Botynella quinquepunctata Weise, 1891:287. Distribution: Cuba.

Structures of this genus are similar to those of Bura, except for the elongate labium (Fig. 1); antenna with a broader, more robust basal segment (Fig. 5); prosternal process narrower, shorter, less protuberant (Fig. 7). Figures 8 and 9 illustrate the similarity in clypeal structure between Botynella and Psorolyma.

## Geodimmockius Chapin

Geodimmockius Chapin, 1930:489. Type species: Geodimmockius explanatus Chapin, by monotypy.

A monotypic genus known only from Cuba, Geodimmockius is an extremely distinctive taxa readily recognized by characters given in the key.

## Psorolyma Sicard

Psorolyma Sicard, 1922:358. Type species: Psorolyma maxillosa Sicard, by monotypy.
Psorolyma maxillosa Sicard, 1922:360. Distribution: Puerto Rico.
Psorolyma sicardi Gordon, 1974:229. Distribution: Jamaica.


Figs. 1-7. Botynella quinquepunctata, labium. 2. Bura cuprea, labium. 3. Bura cuprea, antenna. 4. Psorolyma maxillosa, antenna. 5. Botynella quinquepunctata, antenna. 6. Bura cuprea, prosternal process. 7. Botynella quinquepunctata, prosternal process.


Figs. 8-13. Head views. 8. Botynella quinquepunctata. 9. Psorolyma cyanella. 10. Psorolyma maxillosa (male). 11. Psorolyma doyeni. 12. Psorolyma sicardi. 13. Psorolyma baorucensis.

Psorolyma cyanella Gordon, 1974:230. Distribution: Hispaniola.
Psorolyma doyeni, new species. Distribution: Hispaniola.
Psorolyma baorucensis, new species. Distribution: Hispaniola.
This genus is typically cocciduline in structures such as the antenna (Fig. 4), but is atypical in having male genitalia with asymmetrical basal lobes as illustrated in Figures 18 and 22. Each known species has differently formed clypeal apices as in Figures 9-13. Except for the genitalia of $P$. maxillosa, both male and female genitalia are very uniform in appearance, but the siphonal apex is characteristic for each species.

The first paper in this West Indian series (Gordon, 1974) was a revision of Pso-


Figs. 14-17. 14. Bura cuprea, head. 15-17. Habitus views. 15. Geodimmockius explanatus. 16. Botynella quadripunctata. 17. Psorolyma cyanella.
rolyma in which the genus was redescribed and two species were added. Two additional species were recently discovered in the collection of the University of California, Berkeley; therefore the existing key is modified, and these species are described. See Gordon (1974) for a generic description and illustrations of previously described species.


Figs. 18-21. Psorolyma doyeni. 18-20. Male genitalia. 21. Female genitalia.

Host information for members of Psorolyma consists of a single bit of data associated with specimens of Psorolyma maxillosa Sicard, as follows; "On coffee feeding on Toxoptera aurantiae." Toxoptera aurantiae (Boyer de Fonscolombe) is a widespread aphid species, and it appears possible that Psorolyma species are, in general, aphid predators.

Type specimens are deposited in the collections of the California Academy of Sciences (CAS), San Francisco, California; M. Ivie (MI), Bozeman, Montana; University of California, Berkeley (UCB); and the National Museum of Natural History (USNM), Washington, D.C.

## Psorolyma doyeni, new species

Description: Holotype male, length 2.4 mm , width 1.7 mm . Form oval, somewhat elongate, widest at middle of elytra. Color black, head and pronotum with green sheen, elytron with strong purple sheen; mouthparts, basal 8 antennal segments, tibia, tarsus yellow; apical 3 antennal segments, trochanter, femur dark brown. Head with clypeal apex broadly, distinctly emarginate, anterior angle abrupt (Fig. 11); eyes separated by $2.8 \times$ width of eye; surface smooth, polished, very finely punctured, punctures separated by a diameter or slightly more. Pronotum with surface slightly alutaceous, shiny; punctures equal in size to head punctures, separated by 1 to 2 times a diameter. Elytron with surface slightly alutaceous, shiny; punctures much coarser than on head, size slightly irregular, separated by a diameter or less. Epipleuron obliquely inclined. Apical margin of prosternum protruding slightly at middle. Postcoxal line on metasternum beginning in deep pit. Abdomen with postcoxal line on 1 st sternum deeply impressed in basal $1 / 4$, not beginning in a pit; apex of 5 th sternum truncate. Genitalia simple, basal lobe as long as paramere, apex slightly asymmetrical (Fig. 18); sipho slender, unmodified (Figs. 19, 20).

Allotype: Length 2.5 mm , width 1.7 mm . Similar to male except apex of 5th sternum rounded. Spermathecal capsule elongate, slender, cornu abruptly bent (Fig. 21).

Variation: Length 2.0 to 2.5 mm , width 1.6 to 1.7 mm . Head, pronotum sometimes with purplish reflections mixed with green sheen.

Type material: Holotype: Rep. Dom: La Vega Prov. 24 km S Jarabacoa, 4,000', ex. vegetation, I-2-1987, J. Doyen (CAS). Allotype, 4 paratypes, same data as holotype; 1 paratype, Haiti, 1925 WA Hoffmann, Camp Perrin, July 25; 1 paratype, Dominican Rep, Los Hidalgos, 4-5-VI-1969, Flint \& Gomez. (CAS) (UCB) (USNM).

Remarks. In addition to characters used in the key to species, $P$. doyeni can usually be recognized by the distinct green sheen on the head and pronotum contrasted with the purple sheen of the elytra. The pronotal punctures of both $P$. doyeni and $P$. baorucensis are much finer and less dense than in P. cyanella, the only described species with which they could be confused. Gordon (1974) stated that he had seen 3 specimens of $P$. cyanella that had an atypical clypeal apex. These specimens were not included in the type series of $P$. cyanella and they now prove to be examples of $P$. doyeni.

The species is named for John Doyen, collector of the type series and an eminent coleopterist.

## Psorolyma baorucensis, new species

Description: Holotype male, length 2.0 mm , width 1.8 mm . Form oval, somewhat round, widest at middle of elytra. Color black, head and pronotum with purple sheen, elytron with strong green sheen; basal 8 antennal segments, mouthparts, tibia, tarsus yellow; apical 3 antennal segments light brown; ventral surface, femur dark brown. Head with clypeal apex deeply emarginate, anterior angle abrupt (Fig. 13); eyes separated by $2.4 \times$ width of eye; surface slightly alutaceous, shiny, punctures fine, separated by about a diameter. Pronotum with surface polished, punctures equal in size to head punctures, separated by less than to twice a diameter. Elytron with surface slightly alutaceous, shiny, punctures slightly coarser than on head, uniform in size, separated by twice a diameter. Epipleuron obliquely inclined. Apical margin


Figs. 22-25. Psorolyma baorucensis. 22-24. Male genitalia. 25. Female genitalia.
of prosternum protruding slightly at middle. Postcoxal line on metasternum beginning in deep pit. Abdomen with postcoxal line on 1st sternum deeply impressed in basal $1 / 4$, not beginning in pit; apex of 5th sternum truncate. Genitalia simple, basal lobe slightly longer than paramere, apex slightly asymmetrical (Fig. 22); sipho slender, unmodified (Figs. 23, 24).

Allotype: Length 2.2 mm , width 1.8 mm . Similar to male except clypeal apex not as deeply emarginate and apex of 5th sternum rounded. Spermathecal capsule elongate, slender, cornu abruptly bent (Fig. 25).

Variation: Length 1.75 to 2.3 mm , width 1.6 to 1.8 mm . Head, pronotum sometimes with greenish reflections mixed with purple sheen.

Type material: Holotype: Dominican Republic, Prov. Pedernales, 25 km N Cabo Rojo, $915 \mathrm{~m}, 09$ SEP 1988, wet forest at light \& night beating, M. Ivie, Philips \& Johnson (USNM). Allotype: Rep. Dom: Pedernales Prov., Sierra Baoruca, 31 km N Cabo Rojo, 2,500', XII-29-1986, Doyen and Santiago, Broad leaf mesophyll association (Beating vegetation) (UCB). 6 paratypes, same data as allotype except additional date "XII-30-1986"; 1 paratype, same data as holotype; 1 paratype, Domin. Rep: Prov. Pedernales ca. 35 km N Cabo Rojo, 1,250 m, Las Abejas, 09 SEP 1988, beating veg., M. A. Ivie, T. K. Philips \& K. A. Johnson. (MI) (UCB) (USNM).

Remarks: This species most nearly resembles $P$. doyeni but the head and pronotum usually have a purple sheen and the elytra have a green sheen, a reverse pattern from that of $P$. doyeni; see remarks under that species. In addition, the body form tends to be rounded in P. baorucensis, elongate in $P$. doyeni.

The species is named for the mountains where the type series originated.

## KEY TO SPECIES OF PSOROLYMA

1. Dorsal punctation composed of intermixed coarse and fine punctures; coarse punctures sparse, irregularly spaced; male clypeal apex with strong, triangular projection on each side (Fig. 10); Puerto Rico . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . maxillosa Sicard Dorsal punctation fine, punctures uniform in size or with only slight size differential, not irregularly spaced; male clypeal apex not as described above; not known from Puerto Rico2

2(1). Elytron yellow with 2 black spots; Jamaica . . . . . . . . . . . . . . . . . . . . . . . sicardi Gordon Elytron dark, concolorous; Hispaniola 3

3(2). Clypeal apex nearly truncate, anterior angle broadly rounded (Fig. 9); elytral punctures fine, uniform in size ...............................................cyanella Gordon Clypeal apex distinctly emarginate, anterior angle abrupt; elytral punctation fine, uniform in size, or punctures slightly coarser, size slightly irregular 4

4(3). Clypeal apex strongly emarginate, anterior angle abrupt (Fig. 13); elytral punctation fine, uniform; elytron usually with green surface sheen . . . . . . baorucensis, new species Clypeal apex moderately emarginate, anterior angle less abrupt (Fig. 11); elytral punctation slightly coarser than in baorucensis, punctures slightly irregular in size; elytron usually with purple sheen
doyeni, new species

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# WEST INDIAN COCCINELLIDAE VI (COLEOPTERA): NEW GENERA AND SPECIES OF STICHOLOTIDINI AND A CLADISTIC ANALYSIS OF INCLUDED GENERA 

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Abstract.-Additions to the West Indian fauna of Sticholotidini are Lenasa, n. gen.; Lenasa jayuyai, n. sp.; Neotina schwarzi, n. sp.; Neaptera doyeni, n. sp.; Neaptera cubensis, n. sp.; and Neaptera dissita, n. sp. The first records of Neaptera Gordon from Cuba and Costa Rica are reported, and a new key to all Western Hemisphere genera of Sticholotidini was constructed. A phylogeny of the West Indian Sticholotidini generic fauna is proposed.

The fourth publication in this series (Gordon, 1991) dealt with all West Indian genera and species of Sticholotidini then known. Descriptions and added information are presented herein for one undescribed genus and 5 new species discovered in material examined subsequently.

A generic phylogeny for the West Indian genera of Sticholotidini is proposed using 25 characters. The Scymnillini genus Zilus was used as the outgroup because it has many similarities to most of the West Indian genera of Sticholotidini. Type material is deposited in the collections of the U.S. National Museum of Natural History, Washington, D.C. (USNM), and the University of California, Berkeley (UCB).

The key to genera of New World Sticholotidini (Gordon, 1991) is modified to include Lenasa, new genus, and the South American genera Glomerella Gordon (1977), Neojauravia Gordon and Almeida (1991), Neotina Gordon (1977), and Nexophallus Gordon (1969).

## KEY TO GENERA OF NEW WORLD STICHOLOTIDINI



Abdomen with 5 visible sterna ....................................................... 3
3(2). Epipleuron foveate for reception of femur; eye completely divided by genal extension; prosternum expanded anteriorly, partially or completely concealing mouthparts; anterior tibia broadly expanded, externally dentate or not
Epipleuron not foveate for reception of femur; eye not completely divided; prosternum not expanded anteriorly; tibia unmodified 5
4(3). Pronotum with sparse, fine pubescence; external margin of anterior tibia not an- gulate Glomerella GordonPronotum without pubescence; external margin of anterior tibia sharply angulate
Eye small, coarsely faceted ..... 7
6(5). Head, pronotum sparsely pubescent; prosternal process short, rectangular
Nesina Gordon
Head, pronotum glabrous; prosternal process oblong, apically rounded ......... .
Lenasa, n. gen.
7(5). Postcoxal line on 1 st abdominal sternum complete
8
Postcoxal line on 1 st abdominal sternum incomplete 9
8(7). Terminal segment of maxillary palpus long, slender, apically acuminate
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Nexophallus Gordon
Terminal segment of maxillary palpus less elongate, apex obliquely truncate
Neaptera Gordon
9(7). Terminal segment of maxillary palpus short, wide . . . . . . . . . . . . . . . . Nelasa Gordon
Terminal segment of maxillary palpus elongate, slender . . . . . . . . . . . . . . . . . . . . . 10
10(9). Body strongly convex, rounded, apex of elytra abruptly descending ventrad; antennal club slender; prosternal process not ridged Neotina Gordon Body normally convex, oval, apex of elytra gradually descending ventrad; antennal club extremely broad; prosternal process heavily ridged
Semiviride Gordon

## Lenasa, new genus

Sticholotidini with form rounded, slightly oval; without pubescence except on clypeus; dorsal surface with metallic sheen throughout; punctation on elytron slightly coarser than on head and pronotum. Head broad; clypeus short, truncate apically, anterior angle rounded (Fig. 1). Eye finely faceted, large; eyes separated by $2^{1 / 2}$ times width of eye; gena strongly extended onto eye, recurved, occupying nearly $1 / 2$ eye. Antenna 10-segmented; club 3-segmented, elongate (Fig. 2). Terminal segment of maxillary palpus short, slightly tapered toward apex (Fig. 3). Prosternum without anterior projection, coxae widely separated by large, protuberant, oblong, apically rounded process strongly ridged on lateral, apical margins; median area convex, with long, sparse setae. Elytron normally curved ventrally; lateral margin with weakly defined bead. Hind (flight) wing present. Epipleuron narrow, feebly descending externally, not foveate for reception of femoral apices. Leg with femur robust, shallowly grooved for reception of tibia; tibia slender, unmodified, not externally dentate, shorter than femur; tarsus cryptotetramerous; tarsal claw with small, acute, basal tooth. Abdomen with 5 visible sterna; 1st sternum with postcoxal line incomplete, not reaching hind margin of sternum, extending along hind margin nearly to lateral margin, slightly, evenly recurved in apical $1 / 3$ (Fig. 4); apex of 5th sternum broadly rounded in both sexes. Male genitalia symmetrical. Female genitalia with unmodified spermathecal capsule (Fig. 5); without infundibulum.

Type species: Lenasa jayuyai, new species.
Lenasa is similar to Semiviride Gordon and Neotina Gordon in the form of the prosternal process, the slightly recurved postcoxal line extended along the hind margin of the first abdominal sternum, and in having a large, recurved genal extension onto the eye. The apical segment of the maxillary palpus is most similar to that of Nelasa. Lenasa can be recognized by the large, oblong, strongly ridged prosternal process similar to that of Semiviride except that the process is narrower with stronger lateral ridges in Lenasa. Food and habitat preferences are unknown. It is presumed that the type specimens were taken by beating vegetation.

The generic name is an arbitrary combination of letters and the gender is feminine.


Fig. 1. Lenasa jayuyai, head.

## Lenasa jayuyai, new species

Description: Holotype male, length 1.6 mm , width 1.4 mm . From rounded, slightly oval. Color black with strong, metallic green sheen on dorsal surface; antenna, tibial apex, tarsus yellow; mouthparts, leg, ventral surface dark reddish brown. Head shiny, surface polished, finely punctured; punctures separated by 1 to 4 times a diameter. Pronotum shiny, polished; punctures equal in size to head punctures, separated by 2 to 4 times a diameter. Elytron smooth, polished, with intermixed fine, coarse punctures; coarse punctures separated by less than to 4 times a diameter; fine punctures irregularly scattered. Postcoxal line on 1 st abdominal sternum long, slightly recurved at apex (Fig. 4). Genitalia long, slender; basal lobe symmetrical, as long as paramere, apical $1 / 3$ slightly spatulate, apex forming short, tapered tube; paramere slender, nearly of equal width from base to apex (Fig. 6); sipho somewhat elongate, apex curved (Figs. 7, 8).

Allotype: Length 1.6 mm , width 1.4 mm . Similar to male; genitalia (Fig. 5) with spermathecal capsule short, abruptly bent medially.

Variation: Length 1.4 to 1.6 mm , width 1.3 to 1.4 mm . The dorsal surface varies slightly in degree of green sheen; some specimens are not as brightly green as described for the holotype.

Type material: Holotype; Puerto Rico, Jayuya, VII 22, 1969, H.\&A. Howden (USNM). Allotype; same data as holotype except date VII 23, 1969 (USNM). Paratypes; 1, same data as holotype, 3, same data as allotype (USNM).

Other material: One female labeled "El Yunque, PR, 17.2.25, HL Dozier" is


Figs. 2-8. Lenasa jayuyai. 2. Antenna. 3. Maxilla. 4. Postcoxal lines on basal abdominal sternum. 5. Female genitalia. 6. Male genitalia, ventral view of phallobase. 7, 8. Siphon of male genitalia.
probably this species. However, it is not designated a paratype because the dorsal surface has a coppery sheen and the elytral punctation is much sparser than is typical of $L$. jayuyai.

Remarks: The species is named for the type locality.

## Neotina Gordon

Neotina Gordon, 1977:213. Type species: Neotina cariba Gordon, by monotypy.
Neotina cariba was described from a single male specimen collected on the Island of Cuba. Neotina schwarzi, a unique male also from Cuba is here described. Thus far the genus is known only from Cuba and may be endemic there. The fauna of the remaining members of the Greater Antilles is relatively well studied at this point, and no specimens of Neotina have been discovered.

## KEY TO SPECIES OF NEOTINA

1. Elytron with dual punctation, coarse punctures widely scattered, separated by 3 to 6 times a diameter, deeply impressed; elytron mostly reddish orange, humeral callus and lateral margin dark cariba Gordon Elytron without dual punctation, punctures fine, dense, separated by one to 4 times a diameter; elytron light brown with greenish sheen ...................... schwarzi, n. sp.

## Neotina schwarzi, new species

Description: Holotype male, length $1.4 \mathrm{~mm}, 1.2 \mathrm{~mm}$. Form nearly round. Color reddish brown; mouthparts, antenna yellow; head dark reddish brown with greenish blue sheen; pronotum dark reddish brown with greenish sheen; elytron light brown with greenish sheen. Dorsal surface smooth, polished. Head finely punctured, punctures separated by 1 to 3 times a diameter. Pronotum with single punctation, coarse punctures slightly larger than head punctures, separated by less than to twice a diameter, fine punctures dense, separated by less than to twice a diameter. Elytron with punctures slightly smaller than coarse pronotal punctures, separated by 1 to 4 times a diameter; lateral elytral margin thin, narrowly flanged. Genitalia lost.

Type material: Holotype; Cuba, Cayamas, 10.3, EA Schwarz Collector (USNM).
Remarks: Neotina cariba has dual punctation on mostly red elytra, and the flanged, lateral elytral margin is thick and wide. Neotina schwarzi has greenish brown elytra with single punctation and a thin, narrow lateral elytral flange. The species is named for E. A. Schwarz, collector of the type specimen.

## Neaptera Gordon

Neaptera Gordon, 1991:309. Type species: Neaptera purpurea Gordon, by original designation.

Three new species are added to the original four described in 1991. One from Costa Rica is the first mainland record of Neaptera, and another is the first record from Cuba.

Gordon (1991) stated that Neaptera, Nelasa, and Paranelasa Gordon had 6 visible abdominal sterna. Previously known genera of Sticholotidini had only 5 visible sterna, therefore this was the first reported occurrence of a significantly different character state. Reexamination of these genera indicates that Neaptera and Nelasa actually have only 5 sterna; many specimens do have the 6th sterna slightly visible, but specimens in a normal condition have only 5 visible sterna. Paranelasa remains
unusual because all specimens consistently have a small portion of the 6th sternum visible.

## KEY TO SPECIES OF NEAPTERA


2(1). Elytron dark reddish brown, lacking metallic sheen; Puerto Rico ....... doyeni, n. sp.
Elytron reddish brown or not, with metallic sheen; not known from Puerto Rico ... 3
3(2). Elytron metallic blue; punctures dense; coarse punctures separated by a diameter or less; Guadeloupe ................................................. korschefskyi (Duverger)
Elytron metallic blue or not; if black with metallic blue sheen, species not from Cuba; punctures not dense; coarse punctures separated by a diameter or more ..... 4

Elytron metallic purple or violet ....................................................... 5
5(4). Species known only from Costa Rica ........................................... dissita, n. sp.
Species not known from Costa Rica .................................................. 6
6(5). Species known only from the Virgin Islands ......................... purpurea Gordon
Species known only from Guadeloupe or Montserrat .................... viola Gordon

## Neaptera doyeni, new species

Description: Holotype male, length 1.3 mm , width 1.0 mm . Color dark reddish brown; dorsal surface lacking metallic sheen; mouthparts, antenna, leg yellow; ventral surface reddish brown. Head smooth, polished, punctures distinct, separated by less than to twice a diameter. Pronotum smooth, polished, punctures finer than on head, separated by 1 to 4 times a diameter. Elytron smooth, polished, surface with faint trace of alutaceous sculpture, punctation dual with sparse, intermixed fine and coarse punctures; coarse punctures separated by 1 to 4 times a diameter. Genitalia with basal lobe shorter than paramere, unmodified; paramere slender, apical setae short, sparse (Fig. 9); sipho lost.

Type material: Holotype: Puerto Rico, Sierra Laquillo, Caribbean Nat. For. Rd. 191, 12 mi S Palmer 2,500', Xii-22-1986, J. Doyen \& J. Santiago collectors, ex dead palm fronds (UCB). Paratype (male); 1, same data as holotype (USNM).

Remarks: Both N. doyeni and N. viridissima have dual elytral punctation, but the coarse elytral punctures are very large and deeply impressed in N. viridissima and comparatively small, feebly impressed in $N$. doyeni, the only other species known from Puerto Rico. The elytra of $N$. viridissima are metallic green while those of $N$. doyeni are dark reddish brown without metallic sheen. In addition, the basal lobe of the male genitalia is broad, apically rounded, and shorter than the paramere in $N$. doyeni; it is slender, apically acute, and longer than the paramere in $N$. viridissima. The species is named for John Doyen, collector of the type series.

## Neaptera cubensis, new species

Description: Holotype female, length 1.4 mm , width 1.0 mm . Dorsal surface with metallic sheen; apical $1 / 3$ of head light reddish brown, posterior $2 / 3$ dark brown, entire head with metallic green sheen; pronotum dark brown with metallic green sheen;


Figs. 9-12. Male genitalia. 9. Neaptera doyeni, phallobase. 10-12. Neaptera dissita. 10. Phallobase. 11. Siphon. 12. Enlarged siphonal apex.
elytron black with metallic blue sheen; mouthparts, apical $1 / 3$ of femur, tibia, tarsus yellow. Head smooth, polished, punctures distinct, separated by less than to twice a diameter. Pronotum smooth, polished, punctures finer than on head, separated by less than to 3 times a diameter. Elytron smooth, polished, surface without trace of alutaceous sculpture, with dual punctation composed of sparse fine and coarse punctures, coarse punctures separated by 1 to 4 times a diameter.

Type material: Holotype; Cuba, Det. by F .W. Nunenmacher, Scymnillus viridimicans Sic., Korschefsky Collection 1952 (USNM).

Remarks: This is the only Cuban species of Neaptera thus far known. The black with metallic blue sheen of the elytron resembles only that of N. korschefskyi from Guadeloupe, but N. cubensis has widely spaced elytral punctation in contrast to the
closely spaced punctures of $N$. korschefskyi. The holotype was identified by Nunenmacher (label data) as Scymnillus viridimicans which it resembles only in dorsal coloration.

The species is named for the type locality.

## Neaptera dissita, new species

Description: Holotype male, length 1.4 mm , width 1.1 mm . Dorsal surface with metallic sheen; apical $1 / 3$ of head light reddish brown, posterior $2 / 3$ dark brown, entire head with metallic green sheen; pronotum dark brown with metallic green sheen; elytron black with metallic purple sheen; mouthparts, antenna yellow; epipleuron, leg paler reddish brown than ventral surface. Head smooth, polished, punctures distinct, separated by less than to 3 times a diameter. Pronotum smooth, polished, punctures finer than on head, separated by less than to 3 times a diameter. Elytron smooth, polished, surface without trace of alutaceous sculpture, with dual punctation composed of sparse, fine and coarse punctures; coarse punctures separated by 1 to 6 times a diameter. Genitalia with basal lobe longer than paramere, lateral margin slightly sinuate; paramere slender, apical setae short, sparse (Fig. 10); siphonal apex drawn out in very slender filament (Figs. 11, 12).

Type material: Holotype; Costa Rica, Turrialba, Heyne, Berlin-Wilm, 900 m V., sp. nov, Sicard det., Korschefsky Collection 1952 (USNM).

Remarks: At present, Neaptera dissita is the only known mainland species of Neaptera. It most closely resembles N. viola from Guadeloupe and Montserrat, but $N$. viola has more closely spaced elytral punctation, the coarse punctures separated by 1 to 3 times a diameter as opposed to 1 to 6 times in $N$. dissita; the elytral metallic sheen is violet, and the basal lobe of the male genitalia is less sinuate.

The species name is from the Latin dissitus, meaning apart or remote, in reference to the mainland type locality.

## PROPOSED PHYLOGENY FOR WEST INDIAN GENERA OF STICHOLOTIDINI

## Classification of Sticholotidini character states

Character states are listed below with the primitive condition first, derived condition second (in brackets). Numbers on the diagram (Fig. 13) refer to the following characters. Characters are polarized using the Scymnillini, genus Zilus, as the outgroup.
(1) Antenna with both segments 5, 6 longer than wide (both segments 5,6 wider than long)
(2) Antennal club short, broad (elongate, slender)
(3) Eye small, coarsely faceted (large, finely faceted)
(4) Eye completely divided by genal extension (not completely divided by genal extension)
(5) Genal extension long, $1 / 4$ or more width of eye (genal extension short, less than $1 / 4$ width of eye)
(6) Terminal maxillary segment short (elongate)
(7) Terminal maxillary segment not apically acuminate (acuminate)


Fig. 13. Proposed phylogeny of West Indian genera of Sticholotidini. Numbers refer to list of characters; convergent characters are in brackets, reversals are indicated by an X .
(8) Head entirely pubescent (not pubescent)-most genera have some clypeal hairs and/or scattered pubescence near the eye
(9) Pronotum entirely or partially pubescent (not pubescent). Pronotal pubescence occurs in Nexophallus as well as in the outgroup, but the arrangement and type of pubescence are completely different, therefore pronotal pubescence in Nexophallus is considered derived.
(10) Elytron gradually descending ventrally in apical $1 / 3$ (abruptly descending ventrally in apical $1 / 3$ )
(11) Lateral margin of elytron with weakly defined marginal bead or without bead (lateral margin strongly flanged)
(12) Epipleuron not foveate for reception of femur (foveate)
(13) Prosternum with intercoxal process flat or slightly raised (protuberant)
(14) Prosternum without anterior projection or lobe (with projection)
(15) Lateral margin of prosternal process not or finely ridged, not heavily ridged (heavily ridged)
(16) Anterior tibia simple, unmodified (expanded)
(17) Anterior tibia not externally dentate (dentate)
(18) Tarsal claw simple, lacking basal projection (with basal projection)
(19) Hind (flight) wing present (absent) (character state not ascertained for Parinesa)
(20) Abdomen 5 -segmented (6-segmented)
(21) Postcoxal line on first abdominal sternum incomplete (complete)
(22) Postcoxal line evenly rounded (angulate)
(23) Postcoxal line on first abdominal sternum short, apical portion not parallel to posterior margin of sternum (long, apical portion parallel to hind margin of sternum)
(24) Spermatheca present (absent)-character state in question for Parinesa, holotype not dissected, and for Neotina, female unknown
(25) Infundibulum present (absent) - character state in question for Parinesa, holotype not dissected; and for Neotina, female unknown
were estimated using Hennig 86 developed by James S. Farris. Four alternative phylogenies were generated. The preferred phylogeny, which best fits preconceived notions of the classification, has a length of 32 and a consistency index of 78. Homoplasious characters, with consistency indices in parenthesis, are $2(0.50), 6(0.33)$, $9(0.50), 19(0.50), 21(0.50)$ and 23(0.50). Characters 2, 21, and 23 are convergent; characters $6,9,15$ and 19 are reversals. Character 6 appears as an apomorphy for the group but is secondarily lost twice in Nelasa and Lenasa. Character 9, absence of pubescence, is proposed as an apomorphy for the group although Nexophallus also has significant pubescence. However, this vestiture is different from that found in the outgroup. Nexophallus pronotal vestiture consists of very short, appressed, widely spaced, tapered hairs dispersed over the entire pronotal surface as compared to pronotal vestiture of Zilus which consists of elongate, semierect, dense, uniformly slender hairs usually confined to the lateral $1 / 4$ of pronotum.

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# THE STRIDULATORY MECHANISM OF NERTHRA SAY, A NEW SPECIES, AND SYNONYMY (HETEROPTERA: GELASTOCORIDAE) 

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Abstract.-A stridulatory mechanism is recognized for the first time for the genus Nerthra Say, located in the male genital capsule of all species studied. Nerthra toddi NEW SPECIES replaces Nerthra mexicana, Todd 1955 (nec Melin, 1929). It is compared with Nerthra mexicana (Melin) (=Nerthra usingeri Todd, NEW SYNONYMY), with which it has been confused, Nerthra martini Todd, and Nerthra stygica Say. N. martini, N. mexicana and N. toddi all occur in Mexico, but are not known to be sympatric.

Key Words: Insecta, Heteroptera, stridulation, Gelastocoridae, new species, synonymy.

During the course of independent investigations on the genus Nerthra, the authors concurrently discovered that apparently all species of the genus Nerthra have an unrecognized stridulatory mechanism in the male genital complex (Figs. 1, 2), which is described and discussed below. The orientation and microsculpturing of the stridulitrum varies among species, and may provide a key character for species groups separated on the basis of this and other characters. A detailed examination of the genitalia of all 87 Nerthra species, known from all warm regions of the world except southern Europe, will be required to address this question, a task beyond the scope of this paper.

While investigating the morphology of Nerthra species, one of us (PL) noticed that the syntypes of Nerthra mexicana (Melin) are conspecific with Nerthra usingeri Todd. Todd (1955) said that the females of mexicana and usingeri were separable only by distribution, however both of us have now studied Melin's type of mexicana, a series of usingeri, and the species Todd described as mexicana (the latter two based primarily on male characters) and find that both males and females are clearly separable. Below we propose the name Nerthra toddi new species to replace Nerthra mexicana, Todd (nec Melin), and consequently Nerthra usingeri Todd 1954 must fall as a junior synonym of Nerthra mexicana (Melin) 1929.

## Nerthra toddi, new species

Figs. 4, 6, 9, 12-14
Nerthra mexicana, Todd, 1955, nec Melin, 1929. Univ. Kansas Sci. Bull. 37:356357, figs. 43, 94. (in part)
Nerthra mexicana, Todd, 1957. Proc. Ent. Soc. Wash. 59:149
Nerthra mexicana, Todd, 1961. Proc. Hawaiian Ent. Soc. 17:470.
Nerthra mexicana, Polhemus, 1972. Proc. Ent. Soc. Wash. 74:309.



3


Figs. 1, 2. Nerthra spp., male abdominal terminalia, showing stridulatory mechanism. 1. N. mexicana (Melin), genital segments; stridulitrum, four longitudinal striate rows. 2. N. fuscipes (Guerin), proctiger, right lateral view; plectrum, sclerotized posteroventral rim of proctiger. Legend: proctiger, p ; right paramere, r ; hypandria, h .
Figs. 3, 4. Nerthra spp., female abdominal terminalia, ventral view. 3. N. mexicana (Melin). 4. N. toddi, n. sp.

Redescription (all measurements in mm).-Coloration: Ground color light brown to blackish brown; darker specimens with most of frons brown, posterior lobe of pronotum with seven yellowish brown fascia; scutellum medially brownish in darker specimens, hemelytra mottled with yellowish brown; posterior third of each connexival segment yellowish. Venter mostly dark brown, mottled with yellowish brown; genital segments mostly yellowish. Legs yellowish, annulated with brown. Structural characteristics: Male, length $6.30-7.67 \mathrm{~mm}$, width of pronotum $4.38-4.93 \mathrm{~mm}$; width of abdomen 4.38-5.07 mm. Female, length 6.17-6.44 mm; width of pronotum $3.97-$ 4.52 mm ; width of abdomen $3.84-4.52 \mathrm{~mm}$. Head anteriorly with three small apical tubercles, two superapical tubercles and two or three marginal tubercles on each side, the latter about equal in size, and several small tubercles on frons in longitudinal row; slight excavation between eye and lateral tubercles; ocelli present. Pronotum widest at level of the transverse furrow, about equal to width of abdomen; lateral margins straight medially, convergent on anterior third and posterior sixth; posterior margin sinuate. Scutellum wider (2.06) than long (1.51), depressed at basal angles, with a weak tumescence on each side of midline. Hemelytra extending beyond apex of abdomen; membrane broad, prominent; lateral margin of embolium slightly curved, faintly sinuate, not expanded. Connexiva thinly exposed in males; thinly to broadly exposed in females. Abdominal sternites of female asymmetrical, 6 and 7 fused but demarcated by a weak suture line; sternite 7 with shallow transverse depression on left side of midline, with adjacent strong lateral tumescence near left margin, and another smaller depression on right side anterad of small tumescence near right posterior margin (Fig. 4). Male hypandria distally as shown in Figure 6; right paramere elongate, with stout lateral spur near middle (Fig. 9).

Diagnosis. - Nerthra toddi, n. sp. belongs to the stygica group, established by Todd (1955:346), which includes, in addition to toddi, martini Todd, mexicana (Melin) and stygica Say. N. toddi can be most easily separated from the closely related $N$. mexicana (Melin) by the differently shaped male hypandria (Figs. 6, 7) and right parameres (Figs. 9, 10) and differently shaped female segments $5-7$ (Figs. 3, 4). In females of toddi the depression on the left side of sternite 7 is much shorter and shallower and the adjacent tumescence is larger than in N. mexicana (Melin).
$N$. toddi can be separated from N. martini Todd by differences in the male hypandria (Figs. 5, 7) and right parameres (Figs. 8, 9), and differently shaped female segments 5-7 as illustrated by Menke (1979). Females of martini have the posterior margin of sternites 6 and 7 more V -shaped than in toddi. The geographic range of these two species is widely separated, as martini occurs primarily in California, southern Nevada and southern Arizona and barely ranges into Mexico (Polhemus 1972), whereas toddi is known only from eastern and southern Mexico.
$N$. toddi is easily separated from N. stygica Say by the coriaceous and fused hemelytra of the latter; the other species of the group have normal wings with a distinct membrane. There are also slight differences in the male genitalia (Fig. 11), and differently shaped female segments $5-7$ as illustrated by Todd (1955). In females of stygica the posterior margin of sternite 7 is much more V -shaped than in toddi.

Type-material. - Holotype, male: MEXICO. Chiapas: Rio Sesecapa, CL 1248, XII-19-1969, J. T. Polhemus (USNM). Paratypes as follows: Chiapas: 1 female, same data as holotype; 1 female, Puente la Flor, CL 1247, XII-19-1969, J. T. Polhemus (JTPC). Mexico: 3 males, 3 females, Tejupilco, Dist of Temascaltepec, Alt 1,340 m,


Figs. 5-11. Nerthra spp., distal parts of right male parameres and hypandria. 5-7. Hypandria. 5. N. martini Todd. 6. N. toddi, n. sp. 7. N. mexicana (Melin). 8-11. Parameres. 8. N. martini Todd. 9. N. toddi, n. sp. 10. N. mexicana (Melin). 11. N. stygica Say.

VI-VII-1933, H. E. Hinton (SEMK, JTPC). Oaxaca: 1 female, 1 nymph, Tequisistlan, CL 1066, IV-30-1964, J. T. and M. S. Polhemus (JTPC). San Luis Potosi: 1 male, 2 nymphs, El Salto, VI-19-53, Univ. Kans. Mex. Exp. (SEMK). Tamaulipas: 1 male, 14 mi E of Tamazunchale, CL 526, I-8-1971, J. T. and M. S. Polhemus (JTPC); 1 male, 1 female, 5 mi N of Tamazunchale, stop 76, XII-22-1948, H. B. Leech (CAS, JTPC).

Discussion. - In the mixed series of "mexicana" described by Todd (1955), it appears that only the female paralectotype (apparently the female shown in fig. 94 of his monograph) belongs to mexicana (Melin) which is the same as his usingeri;
the others consist of a series of three males and three females that are named as paratypes of the new species toddi described above. Todd's description is quite adequate except for the female, which is figured here (Fig. 4) and compared to the true mexicana (Fig. 3). Females of the two species may be separated by the deeper, longer depression on the left side of sternum 7 of mexicana. The males are easily separated by the differently shaped right male parameres as shown by Todd (1955: figs. 43, 141) and our Figures 9 and 10.

## Nerthra mexicana (Melin)

Figs. 1, 3, 7, 10
Mononyx mexicanus Melin, 1929. Zoologiska Bidrag Frȧn Uppsala, 12:187-188, figs. 80-83. Lectotype, male, here designated, Mexico, Salle, in Stockholm Museum.
Nerthra usingeri, Todd, 1954. Pan-Pac. Entomol. 30:116-117, fig. 2. NEW SYNONYMY.
Nerthra mexicana, Todd, 1955. Univ. Kansas Sci. Bull. 37:356-357. (in part)
Nerthra usingeri, Todd, 1955. Univ. Kansas Sci. Bull. 37:360-362.
Nerthra usingeri, Todd, 1961. Proc. Hawaiian Entomol. Soc. 17:474.
Nerthra usingeri, Todd, 1978. Proc. Entomol. Soc. Wash. 80:313.
Material examined.—UNITED STATES: California: San Bernardino Co.: 1 male (holotype of Nerthra usingeri), Nr. Parker Dam. IV-12-52, R. L. Usinger (CAS); 1 female (allotype of Nerthra usingeri), 3.5 mi N Cross Roads, IV-12-52, J. D. Lattin (CAS); 1 male, 2 females (paratypes of Nerthra usingeri), same data (UCB, JTPC); 2 females, 10 mi NE Earp, I-26-57, Menke \& Stange (SEMK). MEXICO: Jalisco: 1 female, Atentique, XII-5-48, E. S. Ross (JTPC); 3 males, 11 females, 9 nymphs, Rio Tomatlan, CL 736, VI-9-1975, J. T. Polhemus (JTPC). State unknown: 2 males (lectotype, paralectotype), 1 female (paralectotype), Salle (SMNH).

Discussion. - Todd (1955) noted that the syntype series of Mononyx mexicana (Melin) consisted of three specimens; he apparently studied only one female, which he refers to as the type, however as it did not have a lectotype designation it was only a syntype. We have before us three syntypes, two males and female, and here designate one male as lectotype, and the others as paralectotypes.

For comparative notes, see discussion under $N$. toddi, n. sp.
It is indeed curious that $N$. mexicana has a disjunct distribution bisected by that of $N$. martini. N. mexicana is known in the United States only from one locality along the Colorado River at low elevation (ca. 100 masl.) about 400 km from the delta at the head of the Sea of Cortez, and in Mexico is definitely recorded only from two localities in the state of Jalisco, both near the sea (see above, and Todd, 1978). $N$. martini is known mainly from mountain canyons (although it occurs in the Los Angeles basin, CA) and inland localities at moderate elevations, so would seem to be slightly more cold adapted than mexicana. The samples are not yet numerous enough to draw definite zoogeographical conclusions, but the few we have suggest both ecological and altitudinal habitat partioning.

Stridulatory mechanism. - All species studied of the genus Nerthra possess a stridulatory mechanism in the male genital capsule. The mechanism consists of a rastrate area on a dorsally oriented portion of the sternum of abdominal segment 9 (genital


Figs. 12-17. Nerthra spp., male abdominal terminalia, showing stridulatory mechanisms. 12-14. SEM photographs of $N$. toddi, n. sp., dorsally oriented part of tergum IX, showing stridulitrum. 15-17. Photomicrographs of Nerthra spp., showing transversely oriented striate rows of stridulitrum. 15, 17. N. hamata Todd. 16. N. mixta (Montandon).
capsule) (Figs. 1, 12-17) and the sclerotized posterior margin of the cup-shaped segment X (proctiger or anal cone, Figs. 1, 2). The proctiger is attached to segment IX by thick membranes surrounding the base, permitting considerable longitudinal movement. In dissected specimens muscles or tendons can be pulled with fine forceps to create a downward pressure and longitudinal movement of the posterior edge of the proctiger on the rastrate region. The muscles associated with the proctiger are apparently attached to the base of the proctiger and extend anteroventrally to the anterior margin of the ninth sternum (Keffer, in litt.). No stridulatory mechanism has been found in females.

The stridulatory mechanism is quite stable within species groups, but differs somewhat between groups. In Nerthra mexicana (Fig. 1), N. toddi, n. sp. (Figs. 12-14), N. fuscipes (Guerin) and many other New World species, as well as the AfrotropicalSE Asian grandicollis group, the striate rows are oriented longitudinally, whereas in $N$. femoralis (Montandon) from Australia, N. mixta (Montandon) (Fig. 16) and N. hamata Todd (Figs. 15, 17) from New Guinea, as well as most of the other species of the Melanesian region, the striate rows are more transverse. Whether or not the genus Nerthra should be divided into several genera, based on differences in somatic characters as well as the morphology of the stridulatory mechanisms, is a question that will be addressed in a future work. Should it be necessary to divide the genus, six generic names are available, all now in synonymy with Nerthra.

Sound produced by stridulation in these bugs has never been heard by humans to our knowledge. It is possible that stridulation occurs during copulation when the paramere and hypandrium are connected to the female, providing vibration stimulus. This modality has been hypothesized by Eberhard (1985:164-165) for moths and wasps having apparent stridulatory structures in the male genitalia.

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# A NEW SPECIES OF OCTOTOMA CHEVROLAT, 1837, FROM GUATEMALA (COLEOPTERA: CHRYSOMELIDAE, HISPINAE) 

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#### Abstract

Octotoma puncticollis, new species, is described. A partial revised key to Octotoma species is presented.


Key Words: Octotoma, Hispinae, new species.

I recently received four Octotoma sp. from R. S. Anderson, Canadian Museum of Nature (CMNC). These specimens had been examined by E. G. Riley, Texas A\&M University, who thought they were an undescribed species. Having recently published a revision of Octotoma (Staines, 1989) the specimens were sent to me for my opinion. The specimens represent a new species which is described below.

Measurements were taken with an ocular micrometer. Pronotal length and width were taken along the midlines. Elytral width was measured at the humeri. Elytral length was measured from the base to apex. Total length was measured from the base of the antennae to the apex of the elytra. In recording the label data from type specimens, a double slash (//) divides data on different labels.

## Octotoma puncticollis, new species

Elytra black; head black except red between eyes and front; pronotum reddish with black maculae. Head: vertex black, alutaceous; front reddish, red extending upwards to base of eyes; antennae divided by keel; frons punctate; clypeus impunctate; sulcus on inner margin of each eye; antennal segments I-VII reddish, VIII blackish-gray; segment III cylindrical, longer than I or II; IV-VI transverse; VII transverse, wider than preceding, hirsute; VIII elliptical, hirsute. Pronotum: reddish with six black maculae, largest maculae in basal depression, lateral and anterior maculae smaller; margined laterally; tooth in anterior angles; covered with large, deep punctures; anterior margin darkened; pronotal length $0.7-0.8 \mathrm{~mm}$ (avg. $0.75 ; \mathrm{N}=4$ ); pronotal width $1.3-1.7 \mathrm{~mm}$ (avg. 1.5). Scutellum: black, quadrate, alutaceous. Elytra: blackish; longitudinal and horizontal carinae over entire surface; lateral margins dentate; apical margins more dentate; exterior apical angle with flattened lamina; lateral margins distinctly bisinuate; elytral length 4.3-5.0 mm (avg. 4.7); elytral width $2.0-2.3 \mathrm{~mm}$ (avg. 2.2). Legs: punctate on distal half; protibiae flattened; pro- and mesofemora toothed; tibiae reddish at basal third, remainder black; femora reddish at base and apex, blackish near middle. Venter: prosternum sparsely punctate in middle, rugose at sides; abdominal sterna rugose at base and sides, remainder smooth, with white setae. Total length: $5.0-6.0 \mathrm{~mm}$ (avg. 5.6).

Holotype: Guat[emala]: Baja Verapaz; 7.8-8.6 km W Chilascó; 1,560-1,600 m,
26.V.1991, R. Anderson, oak/pine forest, 91-25//Holotype Octotoma puncticollis Staines det. C. L. Staines 1992 (CMNC).

Paratypes: Three specimens with the same data as the holotype but also with Paratype Octotoma puncticollis Staines det C. L. Staines 1992 (2 in CMNC, 1 in author's collection).

Etymology: Combination of punctum (=small hole) and collum (=neck or collar); Latin. The name refers to the distinct punctation on the pronotum.

Discussion: Life history unknown. Immature stages undescribed. Host plant unknown. This species is most similar to $O$. championi Baly and O. plicatula (Fab.). It can be distinguished from $O$. plicatula by the lack of a median sulcus on the head, antennal segment II longer than I, and antennal segment III distinctly longer than II. It can be distinguished from $O$. championi by the uniformly punctate pronotum and by the impunctate clypeus.

Octotoma puncticollis keys to couplet 9 in Staines (1989). The key is modified to include $O$. puncticollis:

$$
\begin{aligned}
& \text { 9(8). Antennal segment II longer than I, III longer than II; lateral margin of elytra } \\
& \text { distinctly bisinuate; head without median sulcus; south Texas to Panama } \ldots \ldots \text {. . . } 10
\end{aligned}
$$

## $9^{\prime}$. Antennal segment I and II equal in length, III barely longer than II; lateral margin of elytra weakly bisinuate; head with median sulcus; eastern half of the United States $\ldots$. . . . . plicatula (Fab.)

10(9). Pronotum uniformly punctate; clypeus impunctate
$10^{\prime}$. Pronotum with disc impunctate; clypeus punctate championi Baly

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# PEMPHIGUS OBESINYMPHAE, A NEW AMERICAN APHID SPECIES WITH DEFENDERS AND SWOLLEN NYMPHS (HOMOPTERA: APHIDOIDEA: PEMPHIGIDAE) 

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#### Abstract

Pemphigus obesinymphae, n. sp., which is closely allied to $P$. populitransversus Riley, was discovered in Arizona and Utah and is described here. The new species forms galls on leaf petioles of Populus fremontii Watson, and produces 1st instar nymphs that possess heavy sclerotization and stout legs. The 2nd and 3rd instar nymphs are swollen and look superficially like wingless adults. The fundatrix, the 1 st instar, 2 nd instar and adult (alate) fundatrigeniae, the 1st instar exule deposited by the alate, the sexupara, and the gall are described. The differences found between the new species and the most similar previously described species, $P$. populitransversus and $P$. knowltoni Stroyan, are given.


The genus Pemphigus (Homoptera: Aphidoidea: Pemphigidae) contains about 65 species and is distributed throughout the northern hemisphere (Blackman and Eastop, 1984). All holocyclic species of Pemphigus form distinctive galls on cottonwood or poplar trees (the genus Populus). Lange (1965) reviewed what was known of the North American species of Pemphigus.

Most species of Pemphigidae (including Eriosomatinae, Pemphiginae, and Fordinae, as in Heie (1980)) show seasonal alternation of host plants. In this type of life cycle, the sexual phase, sexually produced eggs, and first parthenogenetic generations occur on the "primary" host, almost always a woody plant in a taxon that is characteristic for the aphid tribe or subtribe. Migrants from the primary host colonize the secondary hosts, where a series of parthenogenetic generations occurs. Related aphid species often have completely unrelated secondary host-plants; frequently these are herbaceous. Usually the primary host is colonized in autumn and abandoned in spring, and secondary hosts are used in summer.

For example, in the most common Pemphigus life cycle, sexually produced eggs overwinter on bark of a species of Populus (the primary host-plant). In spring, these eggs hatch to give rise to females, called the fundatrices. These initiate formation of galls on newly developing leaves or shoots, then mature and reproduce parthenogenetically within the galls. Typically, all offspring of fundatrices (the fundatrigeniae) are winged parthenogenetic females that migrate to certain herbaceous plants (the secondary hosts), where they deposit all-female broods. These nymphs descend through soil crevices to the roots, where they feed, develop into wingless adults, and reproduce, again parthenogenetically. These and subsequent generations of wingless female on roots are called exules. A series of overlapping generations of exules continues on roots of the secondary hosts until autumn when alate sexuparae are produced. The sexuparae migrate back to cottonwood trees where they enter bark crevices and
produce the dwarf males and sexual females. Sexuales mate and each female deposits a single overwintering egg. The fundatrices hatch from these eggs the following spring, to initiate new galls, thus completing the cycle. In many instances, exule generations may continue on roots of secondary hosts through the winter and into the next season; such life cycles are termed anholocyclic. In Pemphigus betae Doane, single clones have been shown to produce both the specialized wingless morphs that overwinter on roots of secondary hosts as well as the sexuparae that fly back to the primary host-plants in autumn (Moran, 1991). Both root-overwintering morphs and sexuparae are induced by low temperature (Judge, 1967; Moran et al., 1993). The secondary hosts of many Pemphigus species are unknown (Lange, 1965). A few species of Pemphigus, including $P$. monophagus Maxson in North America, omit migration to the secondary host-plants and prolong the gall-dwelling phase on Populus (see Aoki and Kurosu, 1988).

In this paper, we describe Pemphigus obesinymphae, a new North American species that shows unusual features. First, the fundatrigeniae exhibit defensive behavior and morphology during the first instar. Second, these 1st instar nymphs develop into 2nd instar nymphs which are swollen and which resemble small wingless adults. Third, the life cycle is unusual in that migration from galls is delayed until late autumn, overwintering appears to occur only on secondary hosts, and return migration by sexuparae occurs in spring rather than autumn. Results of field and laboratory studies on the behavior and life cycle of $P$. obesinymphae are reported elsewhere (Moran, 1993).

## Pemphigus obesinymphae, new species

Metrical data are indicated as mean and range, based on 10 mounted specimens each for the 1 st instar, 2 nd instar and adult fundatrigeniae and 5 specimens each for the fundatrix, 1 st-instar exule, and sexupara. Measurements are in millimeters.

1. Adult fundatrix (apterous). Body length 3.6 (3.3-3.8). Antenna 4 -segmented; segment III 0.136 ( $0.116-0.176$ ) and IV $0.099(0.096-0.108)+0.018(0.012-0.020)$ in length. Apical rostral segment 0.100 ( $0.098-0.102$ ) long, without secondary setae. Second tarsal segment and femorotrochanter of hind leg 0.146 ( $0.142-0.158$ ) and 0.57 ( $0.54-0.61$ ) long, respectively. Shape and distribution of wax plates as is usual in Pemphigus species (e.g., P. populitransversus, P. dorocola Matsumura (Aoki, 1975). Eighth tergite with $15(10-19)$ setae, genital plate with $37(31-48)$ setae.
2. Fundatrigenia. Only two generations occur in the galls, the fundatrix and her offspring, the fundatrigeniae. All adult fundatrigeniae are winged. Immature fundatrigeniae can be divided into four instars, using the following key:
3. Antenna 4 -segmented; empodial setae long and capitate ........................1st instar

- Antenna more than 4 -segmented; empodial setae short and pointed .................... 2

2. Antenna 5 -segmented; wing pad absent ......................................... 2nd instar

- Antenna 6 -segmented; wing pad present ...................................................... 3

3. Wing pad small, not extending past 1 st abdominal segment .................. 3rd instar
4. Wing pad large, extending past 3 rd abdominal segment ...................... 4th instar

Below we describe the 1 st and 2 nd instar nymphs and adult of the fundatrigenia. First instar fundatrigenia (Fig. 1a, b): Body 0.77 (0.68-0.88) long. Head and thoracic


Fig. 1. Fundatrigenia of Pemphigus obesinymphae: (a) First instar nymph. Scale: 0.2 mm . (b) Wax plates of 1 st instar nymph (pleural and marginal plates on 5 th abdominal tergite). Scale: 0.02 mm . (c) Second instar nymph. Scale: 0.2 mm . (d) Adult antenna. Scale: 0.2 mm . (e) Adult cornicle. Scale: 0.02 mm .
tergites almost wholly sclerotized. Abdominal tergites I-VI each with a pair of marginal, oval or quadrate sclerites and a large transverse sclerite, which are well developed on anterior segments but reduced in size on posterior segments. Antenna 4 -segmented; segments I, II, III and IV with $4,2,3$ and 2 (base) +5 (unguis) setae, respectively; longer basal setae on IV 0.010 (0.008-0.012). Length of each segment as follows: I: 0.045 ( $0.038-0.050$ ), II: 0.051 ( $0.048-0.056$ ), III: 0.080 ( $0.070-0.084$ ), IV: 0.130 ( $0.108-0.138$ ); III constricted at middle, sparsely spinose; IV spinose. Primary rhinaria ciliate, 0.009 ( $0.008-0.010$ ) on III and 0.011 ( $0.010-0.012$ ) on IV in axial length. Rostrum reaching hind coxae, at most extending a little beyond them; apical segment conical, 0.082 ( $0.074-0.088$ ) long, without secondary setae. Head ventrally with a pair of thin setae between antennae, the longer one 0.039 ( $0.034-$ $0.044)(\mathrm{N}=8)$. Legs well developed, fore and hind femorotrochanters $0.227(0.196-$ 0.240 ) and 0.263 ( $0.224-0.276$ ) in length, respectively; second tarsal segment with 5 pairs of setae, $0.100(0.080-0.106)$ long on hind leg; empodial setae capitate, extending beyond apices of claws. Abdominal tergites I-VI each with 3 pairs of long, pointed setae on sclerites; the longest seta on III 0.055 ( $0.044-0.064$ ); VII with 2 or

3 pairs of setae; VIII with 2 (rarely 3 ) setae; cauda with a pair of setae; anal plate with 2 pairs of setae. Spinal and pleural pairs of wax plates (Fig. 1b) composed of distinct cells without "central kernel" (cf. Zwölfer, 1957), distinctly demarcated, located posterior to tergal setae, occurring on abdominal tergites V-VII, but pleural plates on VII at times absent (in that case, the number of setae on VII is also 2). Marginal pair of wax plates (Fig. 1b) also composed of distinct cells without "kernel," but not distinctly demarcated, located just behind marginal setae, occurring on abdominal tergites I-VII, but those on anterior segments usually indistinct. Cornicle ringlike.

Second instar fundatrigenia (Fig. 1c): Body 1.17 (0.98-1.32) long. Abdomen often swollen, 0.70 ( $0.48-0.93$ ) wide. Ratio of abdomen width to body length 0.539 ( $0.440-$ 0.631 ) for 34 specimens without the next instar cuticle developing inside ( $44 \%$ had the ratio larger than 0.55 ). Head and prothorax wholly sclerotized as in the 1 st instar. Mesothoracic tergite with a large transverse sclerite mesially and a pair of sclerites marginally. Metathoracic tergite with a pair of sclerites mesially and a pair of small sclerites marginally. Abdominal tergites membranous, sometimes with small sclerites. Antenna 5-segmented; apical segment 0.115 (0.110-0.124) +0.029 (0.024-0.034) long. Apical segment of rostrum 0.080 ( $0.076-0.084$ ) long, without secondary setae. Femorotrochanter and 2nd tarsal segment of hind leg 0.297 (0.288-0.312) and 0.116 (0.112-0.122) in length, respectively. Empodial setae short and pointed. Abdominal tergites with short setae, longest seta on tergite III 0.012 (0.010-0.014). Wax plates distinctly demarcated, composed of indistinct cells; marginal pair of plates on all thoracic tergites and abdominal tergites I-VII; spinal pair of VII (rarely spinal pair on VII are divided into 4); spinal and/or pleural small plates rarely appearing on other abdominal tergites. Cornicle ringlike.

Adult fundatrigenia (alate) (Figs. 1d, e, 3a): Body 2.2 (1.9-2.5) long, Antenna (Fig. 1d) 6 -segmented, the flagellar segments together $0.58(0.52-0.62)$; the length of each segment as follows: III: 0.162 ( $0.140-0.184$ ), IV: 0.081 ( $0.076-0.088$ ), V: 0.123 ( $0.108-0.132$ ), VI: $0.182(0.172-0.192)+0.028$ ( $0.020-0.036$ ). Antennal segment III shorter than IV + V together, which are slightly shorter than or as long as VI. Primary rhinarium of $V$ rather large and quadrate, 0.035 ( $0.026-0.040$ ) in axial length; that of VI very large, 0.066 ( $0.056-0.080$ ) in axial length. Antennal segment III with $3-6$ secondary rhinaria, of which the most basal is 0.054 ( $0.044-0.066$ ) from basal articulation of segment, distal or basal to the small tooth-like process near base; $0-$ 1 (usually 0 ) secondary rhinaria on IV and V, 0 on VI. Secondary rhinaria normal in type, extending at most round a fraction more than half the circumference of segment III; rarely 2 adjoining rhinaria forming a double-sized rhinarium. Setae at apex of antennal segment $V$ maximally 0.012 ( $0.010-0.014$ ) long, about 0.38-0.64 as long as basal articular diameter of V. Apical segment of rostrum 0.092 (0.0880.096 ) long, without secondary setae, approximately about $1 / 2$ as long as 2 nd segment of hind tarsus. Small oval to transversely elongate spinal wax plates on abdominal tergites I-VI and a large elongate one on VIII, but plates on posterior tergites (except on VIII) reduced in size and often disappearing. Cornicle ringlike; only half of the "ring" sclerotized. Eighth tergite with 5 (4-7) setae; genital plate with 33 (29-37) setae. Second segment of hind tarsus 0.183 (0.174-0.196) long.
3. First instar exule (Fig. 2a). The exule nymphs are deposited by the fundatrigenia. Body length 0.51 (0.48-0.56). Antenna 4-segmented; segments I, II, III and IV with

b


Fig. 2. (a) Wax plates of 1 st instar exule of Pemphigus obesinymphae (spinal and pleural plates on 3rd and 4th abdominal tergites). Scale: 0.02 mm . (b) Antenna of adult sexupara of Pemphigus obesinymphae. Scale: 0.2 mm .
$4,2,3$ and 2 (base) +5 (unguis) setae, respectively; longer basal setae on IV 0.016 (0.014-0.018). Length of each segment as follows: I: 0.038 (0.036-0.038), II: 0.040 (0.040-0.042), III: 0.041 ( $0.040-0.042$ ), IV: 0.072 ( $0.070-0.074$ ). Segments III and IV weakly spinose. Primary rhinaria fringed with distinct cilia, ca. 0.008 on III and 0.012 ( $0.010-0.016$ ) on IV in axial length. Rostrum extending beyond hind coxae, but not reaching wax plates on abdominal tergite III; apical segment 0.064 (0.062$0.066)$ long, without secondary setae. Apical setae on tibia similar to others on tibia. Second tarsal segment with 5 pairs of setae, 0.059 ( $0.056-0.064$ ) long on hind leg; empodial setae pointed, not reaching the apices of claws, 0.013 ( $0.012-0.014$ ) long on hind tarsus. Hind femorotrochanter 0.148 (0.144-0.152) long. Abdominal tergites

I-VI each with 3 pairs of setae, VII with 2 pairs of setae, VIII and cauda each with a pair of setae, anal plate with 2 pairs of setae; longest seta on tergite III ca. 0.014. Wax plates distinctly bordered, composed of separated round cells each with a central kernel; a tergal seta occurring on each plate. Spinal plates on abdominal tergites IIIVII, pleural ones on III-VI. Cornicle absent.
4. Adult sexupara (alate) (Fig. 2b). Body 2.0 (1.8-2.1) long. Antenna 6-segmented, the flagellar segments together 0.53 (0.49-0.57); the length of each segment as follows: III: 0.178 ( $0.156-0.192$ ), IV: 0.089 ( $0.080-0.096$ ), V: 0.095 ( $0.088-0.104$ ), VI: 0.141 $(0.132-0.152)+0.031(0.028-0.032)$. Primary rhinarium normal in type, ciliated, 0.018 ( $0.014-0.024$ ) on V and 0.018 ( $0.016-0.020$ ) on VI in axial length. Antennal segment III with 5-9 secondary rhinaria (mode 6), of which the most basal is 0.060 (0.054-0.066) from basal articulation of segment; number of secondary rhinaria on IV 2-3 and on V and VI 0. Secondary rhinaria slender, not fringed with cilia, extending round a fraction less than half the circumference of segment. Setae at apex of antennal segment V maximally 0.013 ( $0.012-0.014$ ) long; basal articular diameter of V 0.016 (0.014-0.016). Apical segment of rostrum 0.090 ( $0.082-0.098$ ) long, without secondary setae. Small oval to transversely elongate spinal wax plates on abdominal tergites I-V and a large on VIII, but plates on IV and V often faint. Cornicle absent. Eighth tergite with 4 or 5 setae; genital plate with 21 (20-22) setae. Second segment of hind tarsus 0.173 ( $0.164-0.184$ ) long.
5. Gall (Fig. 3d). The galls are formed on the petioles of late flushing leaves; most are adjacent to the leaf blade. The shape is roughly spherical, with the lips of the gall slit sometimes bulging outward. Diameters of mature galls ranged from 8 to 16 (mean 13.8). Walls of mature galls are approximately 1.5 thick. The gall slit is irregular in shape and extends along the equator of the gall for about $1 / 3$ of the circumference, with the petiole and leaf blade at the poles. The lips remain closed along most of their length until the emergence of the adult fundatrigeniae. However, each gall has a single, round ostiole, 1.2 in diameter; this may occur anywhere along the slit.

Material examined: All collections of $P$. obesinymphae were from petiole galls on Populus fremontii Watson in Arizona and Utah, USA, and were taken between 15 July 1991 and 31 July 1992. Arizona locations include: Santa Cruz County: Sonoita, Canelo (Audubon Research Ranch), Patagonia; Cochise County: Portal (Southwest Field Station); Graham County: Thatcher; Pima County: Tucson (Molino Basin, Santa Catalina Mtns.). The Utah localities include Salt Lake County: Salt Lake City (City Creek Canyon) and Davis County: Uintah (Weber River). Some alates that emerged from galls were confined in vials, and their 1st instar offspring were obtained.

The holotype is an alate fundatrigenia, containing embryos, collected from Populus fremontii by N. A. Moran at Patagonia on 13 October 1991. The paratypes are two adult fundatrices collected at Patagonia on 13 October 1991, two fundatrices collected at Patagonia on 8 September 1991 and 19 October 1991, one fundatrix collected at Portal on 16 September 1991, five emigrants collected at Patagonia on 25 August 1991, six emigrants collected at Patagonia on 13 October 1991, ten 1st instar fundatrigeniae, 142 nd instar fundatrigeniae, and one 3 rd instar fundatrigenia collected at Patagonia on 13 October 1991, and 12 1st instar exules deposited by emigrants collected at Patagonia on 25 August 1991. All the paratypes were collected from $P$. fremontii by N. A. Moran. The holotype and eight paratypes will be deposited in the U. S. National Museum, Beltsville, Maryland, U.S.A. An additional 16 paratypes


Fig. 3. Primary rhinarium on antennal segment VI of fundatrigenia of (a) Pemphigus obesinymphae, (b) Pemphigus populitransversus, (c) Pemphigus knowltoni. Scale: 0.02 mm . (b and c drawn from Stroyan, 1970). (d) Gall of Pemphigus obesinymphae on Populus fremontii.
will be deposited at the British Museum of Natural History, London and the Canadian National Museum.
Materials of $P$. populitransversus Riley used for comparison were taken from two galls preserved in alcohol; these had been collected by Roy Danielsson from Populus deltoides Marsh at Long Point, Ontario, Canada on 16 July 1986.

## DISCUSSION

## Taxonomy

Pemphigus obesinymphae, n. sp. is closely related to Pemphigus knowltoni Stroyan and, especially, to Pemphigus populitransversus Riley. These species can be easily distinguished from the other known gall-forming Pemphigus species because the adult fundatrigeniae of all three species have a huge primary rhinarium on the last antennal segment (Stroyan, 1970; Palmer, 1952; Fig. 3a-c). We hypothesize that the three constitute a monophyletic species group within the genus Pemphigus. Both P. obesinymphae and $P$. populitransversus form galls only on Populus fremontii, whereas $P$. knowltoni uses only Populus angustifolia. The three species differ in antennal morphology in the adult fundatrigeniae (Table 1). When adult fundatrigeniae are not present, the presence of a gall ostiole and morphological features of the 1st and 2nd instar fundatrigeniae can be used in order to distinguish $P$. obesinymphae and $P$. populitransversus in galls on Populus fremontii (Table 1).
Table 1. Comparison of features of Pemphigus obesinymphae, Pemphigus populitransversus, and Pemphigus knowltoni.

|  | Pemphigus sp. |  |  |
| :---: | :---: | :---: | :---: |
|  | obesinymphae | populitransversus | knowltoni |
| Reported geographic range | AZ, UT (likely in NM, CO, northern Mexico) | throughout eastern and western North America | UT (possibly in ID, CO, WY, MT) |
| Primary host | $P$ fremontii | $P$ fremontii | P. angustifolia |
| Gall position on leaf | petioles, near blade | leaf petioles, often at center | leaf blades, along mid-rib |
| Leaves used | late flushing leaves | first flush leaves |  |
| Ostiole | present | absent | * |
| Life cycle |  |  |  |
| Sexuparae colonize primary hosts | spring | autumn | autumn |
| Overwintering | only on secondary hosts | as eggs on primary hosts | as eggs on primary hosts |
| Type of leaves galled | late flush | first flush | first flush |
| Fundatrigenia mature in galls | autumn | summer | summer |
| Secondary host taxa | unknown | various Brassicaceae | unknown |
| Adult fundatrigeniae |  |  |  |
| Relative lengths of ant. seg. III \& VI | III $<$ VI | III $\geq$ VI | III $\geq$ VI |
| \# secondary rhinaria on III | 3-6 | 2-5 | 3-9 |
| \# secondary rhinaria on IV | 0 (usually)-1 | 0-1 | 1-3 |
| Rostrum length of embryos within adult fundatrigeniae | beyond lst segment of fore tarsi, near bases of claws | not beyond 1st segment of fore tarsi | * |
| 1 st instar fundatrigeniae |  |  |  |
| Abdominal tergites | heavily sclerotized |  |  |
| No. setae on anal plate |  | 5-6 | * |
| Pleural \& spinal pairs of wax plates on abd. tergites IV | absent | often present | * |
| 2nd instar fundatrigeniae |  |  |  |
| Body shape | swollen | slender | * |
| Pleural \& spinal pairs of wax plates on abd. tergites IV-VI | none | well-developed | * |

## Biology

The galls of $P$. obesinymphae contained aphids of only two generations: the fundatrix and fundatrigeniae, as is typical of Pemphigus. No apterous fundatrigeniae were found in galls of obesinymphae, although such forms are usual in both Pemphigus spirothecae Passerini and Pemphigus monophagus Maxson, other species that are known to have long-lived galls and defenders or suspected defenders (Aoki and Kurosu, 1986, 1988). The adult fundatrigeniae possessed embryos resembling typical Pemphigus exules. Therefore, this species probably alternates between two different host-plant taxa. Despite considerable searching and attempted transfers to several suspected plants (Chenopodium and Poinsettia species), its secondary hosts are yet unknown. The host alternation shows peculiar seasonal timing: fundatrigeniae fly from galls much later in the season than in other Pemphigus, overwintering occurs on secondary hosts, and sexuparae return to $P$. fremontii in May of the following year, after the first leaves have expanded. Sexuparae were collected from 5-20 May at Patagonia in 1992; they produced sexual offspring of typical appearance for the genus. Hatching fundatrices were collected from the same clusters of sexuales, suggesting that the eggs hatch within a short period rather than overwintering. Hatching fundatrices then establish galls on late flushing leaves; gall establishment was observed at the Patagonia site from 15 May-1 June 1992. The first fundatrigeniae began to be deposited in some galls on 10 June. This life cycle recalls that of Schlechtendalia chinensis (Bell), which also produces sexuparae in spring and which also has eggs that hatch without prolonged dormancy or overwintering (Takada, 1991).
P. obesinymphae exhibits four peculiar features: First, the life cycle is dramatically altered (Moran, 1993), with the result that galls occur only on the late leaves that expand later in the season as the shoots elongate. Most Pemphigus initiate galls on the early leaves; however, Bird et al. (1979) and Faith (1979) reported a dimorphism in the timing of gall initiation within $P$. populitransversus, with one gall type restricted to first flush leaves and a second restricted to late leaves. Second, 1st instar nymphs of the 2nd generation attack predators (Moran, 1993) and have the legs well developed and the tergites heavily sclerotized. Defensive 1 st instar nymphs have been reported in Pemphigus dorocola (Aoki, 1978) and P. spirothecae (Aoki and Kurosu, 1986; Foster, 1990), but their tergites are not so strongly sclerotized as in $P$. obesinymphae. Third, galls have an ostiole, through which defenders enter and exit the gall (Moran, 1993). Ostioles are characteristic of galls of Pemphigus dorocola (Aoki, 1978) and $P$. spirothecae (Foster, 1990), but are not known from other American Pemphigus. Fourth, 2nd and 3rd instar nymphs of the 2nd generation are usually much swollen, and look as if they were wingless adults. Such swollen nymphs are not known from galls of any other Pemphigus species. Why they are so swollen remains to be investigated.

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# A NEW SPECIES OF <br> AMBR YSUS STÅL FROM ASH MEADOWS, NEVADA (HETEROPTERA: NAUCORIDAE) 

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#### Abstract

Ambrysus relictus, n. sp. is described from thermal springs in Ash Meadows, Nevada, and compared to Ambrysus amargosus La Rivers, another thermally endemic species occurring in the same area. The warm spring habitat of the species is discussed, and figures are provided of the dorsal habitus, male abdominal terminalia, and female subgenital plate.


The biota of Ash Meadows, a spring fed desert oasis lying in the Amargosa River basin approximately 90 miles northwest of Las Vegas, Nevada, has long been noted for its high concentration of endemic plants, fishes, snails and aquatic insects. The thirty thermal seeps and springs that emerge in this area harbor the most diverse local assemblage of endemic species found anywhere in the continental United States, including the naucorid Ambrysus amargosus La Rivers, which is confined to Point of Rock Springs (La Rivers, 1953), near the southern end of the oasis. In early 1991 it was brought to our attention by Doug Threloff, the biologist for the Ash Meadows National Wildlife Refuge, that a second population of naucorids was present in a group of springs further to the north. These insects proved to be a new species, and are described herein as Ambrysus relictus. The discovery of this taxon brings the number of thermally endemic Ambrysus known to occur in the Amargosa River system to three, including the aforementioned A. amargosus, plus A. funebris La Rivers, which is found in thermal outflows near Furnace Creek, in Death Valley.

In the description below all measurements given are in millimeters. Specimen repositories are given in the acknowledgments.

## Ambrysus relictus, new species

Figs. 1-3
Description. - Small, ovate, brachypterous, shape as in Figure 1. Length, male 5.34 mm (mean, $\mathrm{N}=10$; min. 5.16, max. 5.66 ), female 5.44 mm (mean, $\mathrm{N}=10$; min. 5.22 , max. 5.72); width, male 3.30 mm (mean, $\mathrm{N}=10$; min. 3.11, max. 3.50), female 3.44 mm (mean, $\mathrm{N}=10$; min. 3.22, max. 3.88), widest across embolium.

Ground color yellowish, with strongly contrasting dark markings on dorsum; faintly shining, head and pronotum shallowly rugulose, pronotum punctate; scutellum and hemelytra thickly set with white punctations; head medially and posteriorly brown; pronotum broadly yellowish to luteous on lateral margins and entire posterior margin;
scutellum dark medially; hemelytra with embolium light on anterior $2 / 3$ to $3 / 4$, light wedge-shaped mark present on inner corium at junction of membrane and outer corium, scattered light markings present on corium and clavus. Venter yellowish, tinged with brown; legs yellowish, spines brown.

Head narrow, deeply set into pronotum, produced anteriorly for $1 / 5$ of eye length, anteclypeal margin almost straight; vertex very slightly domed medially, produced behind eyes for $1 / 2$ of eye length, with numerous short setae laterally along and ahead of eyes; length 1.00 , width through eyes 1.44 . Eyes with many ommatidia, twice as long as wide, with narrow lateral flange; embraced posteriorly by pronotum; length 0.55 , width 0.28 , posterior/anterior interocular space $0.69 / 0.89$. Eyes not raised, almost flat dorsally, forming smooth transition to head; labrum broad, rounded; maxillary plates not prominent.

Pronotum slightly domed, lateral margins slightly convex, smooth, set with long silky setae (often appressed); posterior margin broadly demarcated by weak sulcus; humeral angles obtuse, not sharp; maximum length 1.66 , length on midline 0.94 , width 2.89 . Scutellum triangular, not raised, roughly twice as wide as long, length 0.72 , width 1.55 . Hemelytra long, fully developed, reaching almost to posterior margin of abdomen; embolium weakly expanded, not sinuate posteriorly. Hind wings reduced, costal cell present. Connexival margins of tergites II-III (first two visible) smooth, IV-VI weakly serrate; posterolateral angles weakly spinose.

Ventral surface sparsely set with short appressed setae; propleura not contiguous with prosternum; propleura touching medially, separated there from mesosternum.

Fore femur broad, length/width $=1.28 / 0.89$; tarsi reaching to adjacent proximal part of femur. Middle and hind femora slender, each with two closely set rows of small yellowish spines on posterior surface, one row each at dorsal and ventral edges; middle and posterior tibia with numerous stout spines, distally with two transverse rows of smaller spines.

Male and female abdominal terminalia and genitalia as in Figures 2 and 3.
Holotype, brachypterous male: NEVADA, Nye Co., South Scruggs Spring, Ash Meadows NWR, 710 m , water temp. $33^{\circ} \mathrm{C}$, CL 2715,22 July 1992, J. T. and D. A. Polhemus (USNM).

Paratypes, all brachypterous, all from NEVADA, Nye Co., collected by J. T. and D. A. Polhemus unless otherwise noted: 7 males, 10 females, 3 nymphs, same data as holotype (USNM, JTPC); 9 males, 4 females, North Scruggs Spring, Ash Meadows NWR, 710 m , water temp. $33^{\circ} \mathrm{C}$, CL 2714, 22 July 1992; 4 males, 1 female, Marsh Spring, Ash Meadows NWR, 710 m , water temp. $31^{\circ} \mathrm{C}$, CL 2716, 22 July 1992; 1 male, 1 female, North Indian Spring, Ash Meadows NWR, 710 m, water temp. $31^{\circ} \mathrm{C}$, CL 2717, 22 July 1992 (all JTPC, USNM); 9 males, 8 females, Scruggs Ranch, B. Y.U.- A.E.C. (Mercury, Nevada N.T.S.), collector unknown, 15 March 1962 (USNM); 7 males, 8 females, North Scruggs Spring, Ash Meadows NWR, 27 March 1992, R. S. Zack \& K. A. Rosema (WSUC); 9 males, 4 females, Marsh Spring, Ash Meadows NWR, 27 March 1992, R. S. Zack \& K. A. Rosema (WSUC); 1 male, 1 female, 4 nymphs, Scruggs Spring, Ash Meadows NWR, WDS-A-911, 8 August 1992, W. D. Shepard (WSUC); 3 males, 2 females, 10 nymphs, Indian Spring, Ash Meadows NWR, WDS-A-910, 8 August 1992, W. D. Shepard (WSUC).

Etymology. - The name relictus refers to the relictual nature of this warm spring endemic. Masculine.


Figs. 1-3. Ambrysus relictus, n. sp. 1. Dorsal habitus. 2. Female abdominal terminalia, ventral view. 3. Male abdominal terminalia, dorsal view.

## DISCUSSION

A. relictus, n. sp. differs from $A$. amargosus La rivers in the following respects: the male process is absent, with the sixth male tergite differently formed, having no angle or posterior protuberance as in amargosus (Fig. 3); the female subgenital plate is almost symmetrical, versus quite asymmetrical in amargosus, and is notched apically as in amargosus, but with a slightly different shape along the posterior margin (Fig. 2); the body is smaller and narrower than amargosus; the head is more strongly produced posteriorly than amargosus; and the connexival margins of relictus are smooth on tergites II-III (first and second visible segments) and weakly serrate on IV-VI, versus strongly serrate on IV-VI in amargosus, and non-serrate in A. funebris La Rivers. This set of character states would place relictus in the Ambrysus pudicus group of La Rivers (1953:89).

The speciation of Ambrysus in isolated warm springs throughout the Amargosa River drainage of southern Nevada and the adjacent Death Valley region of California parallels a phenomenon well documented for the desert pupfishes (Williams et al., 1985). A. relictus, n. sp. is the third thermally endemic Ambrysus species now known from the Amargosa system; the spring habitats of the other two species, A. amargosus and A. funebris, were discussed by La Rivers (1949, 1953).

## HABITAT

Ambrysus relictus occurs in a closed basin containing five warm springs: North Scruggs Spring, South Scruggs Spring, Marsh Spring, North Indian Spring and School Spring. All of these springs are small thermal outflows with shallow runs less than one meter across. The insects were found in open reaches that were not covered over with vegetation, and had a marly bottom substrate of partially cemented stones, small pebbles and gravel. Both North and South Scruggs Springs have substantial populations of $A$. relictus, while Marsh and North Indian Springs appear to harbor smaller populations. A. relictus is apparently absent from School Spring, possibly because this spring was seriously disturbed by previous owners.

The spring complex containing $A$. relictus is approximately five kilometers north of Point of Rock Springs, a tightly clustered set of thermal outflows harboring the endemic Ambrysus amargosus La Rivers. This latter taxon has experienced extreme population declines over the past forty years due to habitat alterations associated with water development, and is the only aquatic insect presently held on the Federal Register, where it is listed as threatened. The current status of A. amargosus and the history of its decline was recently reviewed by the junior author (Polhemus, in press).

Although currently abundant, A. relictus must also be considered potentially at risk, since it occurs in a similarly limited thermal spring ecosystem. The springs containing $A$. relictus have been designated as "Desert Pupfish Habitat" by the U.S. Fish and Wildlife Service, since they contain an endemic pupfish in addition to the naucorids, and this should in principle confer the species' habitat some degree of protection. Because of the restricted distribution of $A$. relictus, consideration should be given to it in future decisions concerning resource management activities and planning.

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## NOTES AND COMMENTS

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# VIBRATIONAL SIGNALS ASSOCIATED WITH MATING BEHAVIOR IN THE TREEHOPPER, ENCHENOPA BINOTATA SAY (HEMIPTERA: HOMOPTERA: MEMBRACIDAE) 


#### Abstract

Enchenopa binotata Say is actually a complex of several species of arboreal treehoppers associated with six genera of trees in eastern North America (Wood and Guttman, 1981). Detailed life history and phylogenetic studies suggest that speciation in these treehoppers may have occurred in sympatry (Wood and Keese, 1990; Wood et al., 1990, and references therein). Egg hatch and development are tightly linked to host phenology and mating occurs between individuals that are similar in age. Thus, transfer to a new host with a different seasonal phenology within the same habitat could result in temporal reproductive isolation and genetic divergence. In addition to temporal isolation, Enchenopa occurring on different hosts are behaviorally isolated. Under experimental conditions, Wood and Guttman (1982) found that females mate preferentially with males originating from the female's host plant. Wood and Keese (1990) suggest that development of female preferences after divergence along host plant lines may be an important factor that enhances reproductive isolation. However, the mechanism by which females discriminate among males is unknown.

In some auchenorrhynchous Homoptera (e.g., leafhoppers and planthoppers), mating behavior is mediated by substrate-borne vibrational song (Claridge, 1985a, b). The study of inter- and intraspecific variation in leafhopper and planthopper song has proven useful in resolving taxonomic and systematics problems and in understanding the role of song in mate recognition, reproductive isolation, and mate choice (Claridge, 1990; Heady and Denno, 1991; De Winter, 1992; Hunt et al., 1992; Gillham, 1992). Much less is known, however, about intersexual communication in treehoppers. Recent studies of Strictocephala bisonia Kopp and Yonke (Strübing, 1992) and Spissistilus festinus (Say) (Hunt, 1993) demonstrated that mate recognition and attraction are mediated by vibrational communication. In the present study, $E$. binotata individuals were observed to determine whether vibrational signals are associated with mating behavior.


## MATERIALS AND METHODS

Individual males, females, or precopulatory pairs (see Wood and Guttman, 1982) were collected from a mature redbud tree (Cercis canadensis L.) located in an urban landscape in Lexington, KY. Males and females were housed in separate cages containing potted redbud saplings for a period of $0.5-3 \mathrm{~d}$ before they were observed. Observations were done between July 28 and August 10, 1992. Voucher specimens were deposited in the University of Kentucky insect collection.

Individual males ( $\mathrm{N}=10$ ), females $(\mathrm{N}=10)$, or pairs of males and females $(\mathrm{N}=$
15) were placed on the main stem of a potted redbud sapling and observed for one h. Vibrational signals were recorded by resting a phonograph cartridge (Model 39160 , MCM Electronics, Centerville, OH ) on the stem $3-5 \mathrm{~cm}$ from an individual or pair. Signals were amplified 100 -fold using a preamplifier (Model P-16, Grass Instr. Co., Quincy, MA) and recorded on a digital tape deck (Model DTC-700, Sony Corp., Sun Valley, CA) at 48,000 samples/s. Signals were monitored using headphones. Recorded signals were analyzed using a Macintosh computer equipped with Audiomedia (Digidesign, Menlo Park, CA), Alchemy (Passport Designs, Half Moon Bay, CA), and SoundScope (GW Instr., Somerville, MA) hardware and software. Temperature was maintained at $23^{\circ} \pm 2^{\circ} \mathrm{C}$ during observations. Although experimental approaches will be necessary to demonstrate that the vibrations documented in this study have a communicative function, I tentatively refer to these vibrations as signals, calls or songs.

## RESULTS AND DISCUSSION

Individual males ( $8 / 10$ ) emitted at least one spontaneous call during the observation period. Each of these calls was composed of two sections (Fig. 1). The first section consisted of an amplitude- and frequency-modulated wave train. The second section consisted of 2 to 10 pulses. Emission of calls was associated with abdominal quivering that was readily visible at a distance of $\leq 0.25 \mathrm{~m}$. In addition to these complex calls, males occasionally emitted simple vibrations by striking the stem with their abdomen (not figured). These percussive signals were often emitted in doublets or triplets. Isolated females did not emit complex calls, but they did occasionally emit percussive signals similar to those emitted by males. Four of the 15 pairs of males and females mated and the series of behaviors prior to mating were similar for each pair. Each male that mated emitted at least one call of the type emitted by isolated males before climbing onto the side of the female (see Wood and Guttman, 1982). Each male then emitted a courtship song. A second courtship song was detected immediately before copulation. However, the amplitude of the second song was very low and the identity of individuals that produced these vibrations is not certain. The first courtship song consisted of repeating units each of which was composed of a repeating phrase, a single rumbling-like vibration, and a single wing flick (Fig. 2). The first portion of the repeating phrase consisted of a frequency-modulated vibration. The second portion of the phrase was a vibration that produced a pulsed, "rumbling-like" sound similar to the vibration at the end of a unit. After the phrase was repeated several times, the rumble portion of the phrase continued for several seconds, culminating in a wing flick. Repetition of the entire unit continued for several minutes before the emission of the second courtship song. The second song (not figured) consisted of two alternating vibrations that were frequency-modulated. In each case, the second song lasted less than 1 min and ended when genitalia joined.

In a study of $S$. festinus, Hunt (1993) provided experimental evidence that mate recognition and finding depend on the exchange of vibrational signals between males and females. Males of this species spontaneously emit a calling song. Females readily emit response calls in response to calling males located at distances of $>60 \mathrm{~cm}$. Vibrational exchanges continue while males search for stationary females. The overall structure of spontaneous calls emitted by E. binotata males is similar to that emitted


Fig. 1. Oscillograph (lower) and sonograph (upper) of a spontaneous call emitted by an isolated Enchenopa binotata male.
by $S$. festinus males. Although long-distance vibrational interactions and search behavior were not examined in the present study, it is possible that the spontaneous call and/or percussive signals emitted by isolated E. binotata males and percussive and/or other signals emitted by females might mediate long-distance communication.

Vibrational signals and accompanying male/female interactions displayed by $E$. binotata during courtship appear to be far more complex and ritualized than in $S$. festinus. In S. festinus songs emitted by males and females during courtship do not differ greatly from those emitted during initial exchanges and while males search. In contrast, courtship behavior in E. binotata involves the sequential emission of two highly structured songs, both of which are quite different than the spontaneous call emitted by males prior to courtship. Although correlation of abdominal movement to the production of vibrations suggests that males are the predominant singers during courtship, it is possible that some of these vibrations were produced by the females.

Future studies of E. binotata will employ experimental approaches to determine the role of vibrational signals in mate recognition, finding, and courtship. Also, the


Fig. 2. Oscillograph (lower) showing a single unit of the first courtship song emitted by an Enchenopa binotata male. The unit is composed of repeated phrases (P), a rumbling-like vibration (RV), and a wing flick (WF). Sonograph (inset) of four repeated phrases expanded from the region indicated in the oscillograph. Each phrase $(\mathrm{P})$ is composed of a frequency-modulated vibration (FM) and a pulsed "rumbling-like" vibration (PR).
study of inter- and intraspecific variation in vibrational signals produced by members of the $E$. binotata complex and determination of whether female preference is based on evaluation of male vibrational signals may provide insights into speciation and the basis of premating reproductive isolation in these treehoppers.-Randy E. Hunt, Department of Entomology, University of Kentucky, Lexington, Kentucky 405460091.

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## STRIDULATORY MECHANISMS IN AQUATIC AND SEMIAQUATIC HETEROPTERA

A number of new discoveries of putative stridulatory mechanisms in aquatic and semiaquatic Heteroptera are reported here, and previously recognized structures
briefly reviewed. This is a preview of a more comprehensive article (in preparation) giving an overview of communication in aquatic Heteroptera that will include illustrations of the various mechanisms. Publication of these data is needed for a book on the natural history of Heteroptera now in preparation by Schuh, Slater and Stys. Only the suborders Gerromorpha and Nepomorpha are included, as the stridulatory mechanisms of the Leptopodomorpha have been adequately reviewed by Polhemus (1985) and Pericart and Polhemus (1990). A recent review of sound production in aquatic insects by Aiken (1985) dealt with the truly aquatic bugs, but the list below adds two families and nine genera to the taxa of the suborder Nepomorpha possessing stridulatory structures, plus several heretofore unrecognized mechanisms.
Stridulatory mechanisms have two parts, a stationary part characterized as the strigil (alternatively stridulitrum, scraper), and a movable part, the plectrum (alternatively pars stridens, file). Occurrences are listed below by the taxa possessing one or more stridulatory mechanisms, followed by the type of mechanism (strigil first, plectrum second). If the knowledge is published or in press, the citation is given; all others are reported here for the first time, and marked with an asterisk (*).
Sound production has been reported for the family Belostomatidae (Aiken, 1985; Smith, 1982) however the structures have not been found, so this family is not treated below. Sound production in Nepa cinerea L. (Nepidae) was reported by Swinton (1877), who described a supposed pronotum-mesonotum mechanism which was discounted by Handlirsch (1900), thus no plausible mechanism is yet known. While stridulation has been presumed in the corixid subfamilies Cymatiainae and Diaprepocorinae (Aiken, 1985), it has only been demonstrated in the subfamilies Corixinae and Micronectinae (Jansson, 1989), thus only the latter two are included here.

## GERROMORPHA

Gerridae: Metrobates Uhler: about half of the species; males and females. Mechanism: fine ridges on mesoacetabulae; sharp ridge on posterior trochanter (J. and D. Polhemus, 1993).

Veliidae: Angilovelia Andersen: A. y-alba (Paiva) from Asia; males and females. Mechanism: fine ridges on connexival margin; patch of many sharp pegs on dorsum of hind femur (Andersen, 1981).

Veliidae: Paravelia Breddin: P. stenoptera J. and D. Polhemus from Surinam, one undescribed species* from Venezuela; males and females. Mechanism: row of pegs on sides of abdominal sterna III, IV; patch of sharp pegs on hind trochanter ( $P$. stenoptera reported by J. and D. Polhemus, 1984).

Veliidae: Rhagovelia Mayr: R. lugubris Lundblad from Java; males and females. Mechanism: patch of sharp pegs on sides of abdominal sternum III; ridges on hind trochanter (J. and D. Polhemus, 1988).

Veliidae: Stridulivelia Hungerford: all species of the subgenus Stridulivelia; males and females. Mechanism: ridges or denticles on connexival margin; patch of many spinulae or sharp pegs on dorsum of hind femur (Hungerford, 1929).

## NEPOMORPHA

Corixidae: Many genera in the subfamily Corixinae; males and females. Mechanism: sharp ridges on head; roughened patch on fore femur (review by Aiken, 1985).

Corixidae: Many (probably all) species in the subfamily Micronectinae; males only. Mechanism: sharp ridges on abdominal segment 8 (genital capsule; left lobe in Micronecta and Synaptonecta, right lobe in Tenagobia); basal ridges on right paramere (Jansson, 1989; Jansson and Meyer-Rochow, 1990).

Gelastocoridae: Nerthra Say: males of all species worldwide. Mechanism: sclerotized ridges on a dorsally oriented portion of abdominal segment 9 (genital capsule); ridge on proctiger (Polhemus and Lindskog, 1994).

Helotrephidae: Helotrephini, all species of the genera Esakiella China, Helotrephes Stål: Hydrotrephes China (with the possible exception of African species of Esakiella China; Pseudohydrotrephes Poisson not studied); males and females. Mechanism: serrations on costal margin of hemelytra; distal ridge on hind femur (Polhemus, 1990).

Helotrephidae: Helotrephes Stål: H. formosanus Esaki and Miyamoto, H. semiglobosus Stål; males and females. Mechanism: rastrate patch on mesepisternum; fingerlike process on prosternum (review in Polhemus, 1990).

Helotrephidae: Limnotrephes Esaki and China: L. kumaonis Polhemus from India; males and females. Mechanism: rastrate patch on mesepisternum; finger-like process on prosternum (Polhemus, 1990).

Naucoridae: Limnocoris Stål*: all species, all from New World; males and females. Mechanism: sclerotized ridges on lateral margin of at least abdominal sterna II, III; distal ridge on hind femur.

Naucoridae: Ilyocoris Stål: I. cimicoides (L.); Males. Mechanism: sclerotized ridges on abdominal tergite II; sclerotized region on hind margin of abdominal tergite I (Hofeneder, 1937). [Not confirmed as stridulatory, although sound production has been reported, first by Frisch (1727).]

Nepidae: Ranatra F.: all but four New World species. Same mechanism in adults and immatures (Kirkaldy, 1906), possibly the only such occurrence in aquatic insects (Sites and Polhemus, 1994). Mechanism: sclerotized ridges on lateral margin of anterior coxal cavity; ridges on anterior coxae (Torre Bueno, 1905).

Notonectidae: Buenoa Kirkaldy: All species; males only. Mechanism 1: rostral prong; anterior tibial comb. Mechanism 2 (absent in a few species): anterior femoral file; anterior coxal peg (both mechanisms discussed by Wilcox, 1969, 1975).

Notonectidae: Anisops Spinola: All species except B. aglaia Hutchinson; males only. Mechanism: rostral prong; anterior tibial comb (review by Aiken, 1985).

Notonectidae: Anisops Spinola: A. millotti Poisson group* (millotti plus two undescribed spp.) from Madagascar; males and females, sexually dimorphic. Mechanism 1 (males): transverse carinae beneath abdominal connexiva; basal ridge on hind femur (connexival carinae described for millotti by Lansbury, 1966; only tentatively suggested as stridulatory). Mechanism 2 (females): denticles on costal margin of hemelytra; basal ridge on hind femur. Mechanism 3 (females): Sclerotized raised ridge on outer corium of hemelytra; short blunt spines near base of hind femur. (These in addition to the usual mechanism found in Anisops.)

Notonectidae: Anisops Spinola: A. hancocki Hutchinson*, A. psyche Hutchinson*, both from Africa; males only. Mechanism: pegs beneath abdominal connexiva (connexival pegs of both species mentioned by Lansbury, 1966, but not suggested as stridulatory); basal ridge on hind femur (in addition to the usual mechanism found in Anisops).

Notonectidae: Enithares Spinola*: E. biimpressus (Uhler), E. stridulata Brooks, E. tibialis Liu and Zheng, all from Asia, E. nigra Lansbury from New Guinea, an undescribed species from Sumbawa; males and females. Mechanism: ridges beneath abdominal connexiva (illustrated by Lansbury, 1968 for nigra, but not suggested as stridulatory); basal posterolateral ridge on hind femur.

Notonectidae: Martarega White*: One undescribed species from Venezuela; males and females. Mechanism: denticles on costal margin of hemelytra; basal ridge on hind femur.

Pleidae: Plea Leach: P. minutissima Leach; males and females. Mechanism: rastrate patch on mesepisternum; finger-like process on prosternum (Wefelscheid, 1912).John T. Polhemus, University of Colorado Museum, 3115 South York, Englewood, Colorado 80110.

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## A REPLACEMENT NAME FOR MYRMECOMIRIS POLHEMUS AND RAZAFIMAHATRATRA (HETEROPTERA: MIRIDAE)

Polhemus and Razafimahatratra (1990) described the new mymecomorphic mirid genus Myrmecomiris from southwestern Madagascar. Due to a lapsus these authors overlooked the fact that Myrmecomiris had already been proposed as a genus group name by Maldonado (1976) for a mirid in the tribe Herdoniini from Panama, and thus created a primary homonym. To rectify this situation, I propose the replacement genus name Vitsikamiris, n. gen. (from the Malagasy word "vitsika" for ant; gender masculine). The type-species of this monotypic genus, Myrmecomiris madecassa, thus becomes Vitsikamiris madecassa (Polhemus and Razafimahatratra), n. comb.Dan A. Polhemus, Dept. of Life Sciences, Bishop Museum, P.O. Box 19000-A, Honolulu, Hawaii 96817.

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## BOOK REVIEWS

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## Beetle Larvae of the World: Interactive Identification and Information Retrieval for Families and Subfamilies.-J. Lawrence, A. Hastings, M. Dallwitz and T. Paine. 1993. CSIRO Information Services, P.O. Box 89, East Melbourne, Victoria 3002 Australia, CD-ROM disk and 52-page manual. \$240.00.

This system results from the combined application of new computer technologies to the field of systematics. An extensive database of information on larval Coleoptera was compiled using the DELTA (DEscription Language for TAxonomy) system (see Dallwitz, 1980, 1993). The package employs the INTKEY system (Dallwitz, 1993) to allow interactive access to the complete database at each step of the identification process rather than restricting one to a handful of available characters as with traditional, dichotomous keys. In this way the program works as a synoptic key, the advantages of which are discussed by Korf (1972) and Leenhouts (1966). In addition to the natural marriage of computers and synoptic keys, the system benefits from recent advances in CD-ROM technology which make extensive databases and collections of memory-intensive figures available to most PC users.

Already there have been many uses of the DELTA system for generating data matrices and standardized descriptions. These have been largely botanical and viral applications although some exist for hexapods such as Collembola (Christiansen et al., 1990), Hymenoptera (Taylor, 1978, 1979, 1990) and Coleoptera (Britton, 1986; O’Brien and Askevold, 1992). To date, Christiansen et al. (1990) and Taylor (1990) are the only other hexapodan applications also employing INTKEY, the interactive computer identification and information retrieval system.

The heart of the program is a matrix of 180 characters by 385 taxa. Much of the matrix is made up of multistate characters with as many as 17 states. Identifications terminate at various taxonomic levels ranging from family to genus. In Erotylidae, for example, the matrix contains the following four taxonomic groups (i.e., possible determinations): Erotylidae (major part), Dacnini, Megalodacnini and Microsternus. Taxa which vary greatly from instar to instar or which have radically different larval forms (e.g., caraboid, cerambycoid and paedogenetic forms of Micromalthidae) have multiple entries in the database.

Aside from its utility as an identification tool, this expert system also functions as a database of Coleopteran larval information. Six text "characters" in the matrix are used solely for retrieval of information about taxa including geographical distributions, taxonomic synonyms, biology, larval bibliographic references and figures available in the program. The morphological characters can also be searched, sorted and easily accessed using the various functions.

Information in the database is current and as factual as the published literature permits, but due to the present fragmentary state of our knowledge of Coleoptera larvae, some inaccuracies will surely be found for many groups. At present we cannot assess the phylogenetic importance of each character. As such, generalizations about
character states for higher taxonomic groups will be expanded to include additional states as the larvae of other species are described.

This situation, not surprising for a study of this scope on holometabolous larvae, is ameliorated by the INTKEY program with adjustments of "tolerance levels" to give the identification process varying degrees of confidence. If a specimen fails to be determined with relative certainty, the tolerance level can be adjusted so that taxa are not immediately excluded when a conflict between the specimen and the data matrix occurs. Instead, taxa can remain in consideration as potential solutions until their character data conflict with the specimen twice (or as many times as desired). If a character state choice at one step of an identification excludes all remaining taxa, INTKEY automatically adjusts the tolerance level to reconsider those with the fewest conflicts.

Of the 385 taxa included in the matrix, 206 are illustrated. Many figures are familiar as most apparently have been scanned from the major works on Coleoptera larvae such as Costa et al. (1988), Lawrence (1991) and Lawrence and Britton (1991). Computerized coloration of the images makes them three-dimensional and attractive. Three images are scanned from color photographs of larvae in natural surroundings and are quite impressive.

To aid in making determinations, various INTKEY functions assist in understanding the characters. At any point in the determination process, if a character is unclear, one could have the program list the possible states or provide additional notes describing it. The greatest help in understanding the characters, however, is the collection of superb character images available for viewing at any time. Of the 180 characters in the matrix, 110 are illustrated. Most of the images apparently were scanned from Lawrence (1991) and were enhanced with shading and color to make them more attractive and to highlight relevant structures. In two of the images, character states are illustrated effectively with a set of scanning electron micrographs.

My only regret about the graphics is that there are not more taxonomic images included. Many small and obscure groups are not represented. Instead the user is provided with either a screen stating that no figure is available or an image of a superficially similar larva (clearly described as such). An image of a larval Parandra sp. is used to give a superficial representation of eight taxa other than the genus itself. For large or diverse families such as Staphylinidae, illustrations of several additional taxa would be appreciated.

The program facilitates making determinations in many ways. Some of its features are best explained through example. Beginning with an undetermined larva, the Beetle Larvae of the World program has 385 possible determinations. To begin one could use the first true (non-text) characters which are simple and refer to overall size and shape of the specimen. Alternatively, one might recognize that the specimen is, for example, a cucujoid and eliminate all other taxa from the analysis, leaving 77 taxa.

At this point, one could restrict the key to only those characters that are useful in distinguishing the remaining taxa by using the "Best" function which chooses characters with the highest reliability (based on how "clear cut" the states are) and with the best ability to separate the taxa in consideration. The key in the example is thereby reduced to 145 relevant characters and a measurement of the "separating power" of each for the remaining taxa is provided.

To begin using those "Best" characters, one could start with those at the beginning of the list (the best of the best) or with those that are most familiar. Another approach would be to use a suite of characters pertaining to one structure. For example, you might have slide-mounted mandibles in focus at the moment. The "Find" function could quickly identify the nine relevant characters pertaining to mandibles. This could also be accomplished with the "Use" function and a selection of the keyword "mandibles." After scoring the example specimen for the mandibular characters, only three taxonomic determinations remain in consideration: Endomychus, Erotylidae (major part) and Megalodacnini.

At this point, one could move to another convenient suite of characters or pick favorite characters from the list of those remaining. A more efficacious approach would be to use the "Best" function again to list the characters that are capable of separating the few remaining taxa. A total of 58 characters are suggested to further separate the remaining 3 taxa. While scrolling through the list of character names, one may use the ALT +S (tate) function to view a list of the states available for each character.

The example specimen has many conspicuous processes arising from its dorsal and pleural regions so you choose character 113 which asks if such processes occur on the thorax. An affirmative answer eliminates Megalodacnini.

You now ask for the best characters to separate Endomychus from Erotylidae (53 characters are suggested!). You choose character 172 referring to the form of the thoracic spiracles and use the ALT +I (mage) function to see figures of the various states. The specimen has annular-multiforous spiracles, identifying it as an erotylid larva.

This determination could be confirmed by using the "Diagnose" option and by viewing the image of an erotylid larvae. Information about Erotylidae such as distribution, biology, synonymies and larval literature references can be perused in the six text characters of the matrix using the "Describe" function. Hard copies of a session can be obtained by using the various functions provided for customizing output of files and subsequently importing, editing and printing them with wordprocessing software.

To use this system, the following computer equipment is required: an IBM-compatible PC, at least 640 KB of memory, a hard disk, MS-DOS version 3.1 or higher and Microsoft MS-DOS CD-ROM Extensions version 2.1 or higher. A super VGA card and monitor capable of $640 \times 480$ resolution in 256 colors are needed to view the graphics. The video card should comply with the VESA standard or use the TSENG Labs instruction set, although other cards might work satisfactorily. It was reviewed on a Gateway 386/25C system with the following : NEC Intersect CDR84 CD-ROM reader, Adaptec 1542B SCSI board, Adaptec EZ/SCSI software and Gateway 1024 N1 Crystal Scan monitor.

Installation was quick and easy with one exception. There was insufficient space in our system's RAM due to several resident programs and before the program quit and yielded to DOS, it flashed two screens so quickly that neither one could be read nor frozen on the screen despite several attempts. This made diagnosis of the problem more difficult than necessary.

In general this package is nicely produced. The documentation accompanying the
disk consists of a 52 page color booklet which is written clearly and quickly familiarizes one with the program through explanations of the major features and three example identifications. Numerous typographical errors in the manual detract slightly from an otherwise very professional package with nice details right down to the neon purple silk-screened larva on the disk.

The cost ( $\$ 240$ U.S.) is somewhat expensive, a problem likely to be compounded because many potential buyers will be unable to use the program without also purchasing a CD-ROM drive and video board for their systems. This package shows such promise, however, that it seems only a matter of time before that upgrade will be a necessity and a computer will be permanently positioned near the microscope.

The Beetle Larvae of the World interactive program is a perfect demonstration of the practicality and effectiveness of the DELTA and INTKEY systems. The use of synoptic-style keys on a computerized taxon/character database greatly facilitates identification. The core of the program is the most comprehensive collection of character data for Coleoptera larvae "published" to date. The package, further enhanced with many helpful INTKEY functions and a large collection of figures, is an elegant application of new computer technology to the field of systematics.-Joseph V. McHugh, Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999.

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Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico.R. H. Foote, F. L. Blanc and A. L. Norrbom. 1993. Comstock Publishing Associates (a division of Cornell University Press), Ithaca. xii +571 pp . US $\$ 115.50$ cloth.

In the field of agriculture, the true fruit flies (Tephritidae or Trypetidae) are by far the most written about and researched group of Diptera, with citations far in excess of the other major phytophagous groups, namely the Cecidomyiidae and Agromyzidae. Most of that interest is confined to the major fruit pest genera Anastrepha, Bactrocera, Ceratitis, Dacus and Rhagoletis, all of which have been found in North America at some time, even if they are fortunately not all established there. However, most temperate members of the family are not associated with fruit, but with the flowers, or sometimes leaves, stems or roots, of Asteraceae (=Compositae). Most of the 300 species and 56 genera known in North America are Asteraceae-associated, and some of those are actually European species deliberately introduced to help control European plants that have been accidentally introduced into North America. The application of these flies to weed biological control has been possible because most of the Asteraceae-associated tephritids have a remarkably narrow host range, in many cases attacking only a few plants belonging to a single species group, subgenus or genus. Complex behavioral patterns in mate recognition and the use of the host plant as a mating rendezvous site have no doubt facilitated the evolution of many closely related species each with differing ranges of hosts. However, the family $\mathrm{Te}-$ phritidae has been remarkably neglected by the major workers in plant-insect relationships, and most of our knowledge of the biology of the Asteraceae-associated species comes from the work of present or former biocontrol specialists.

This monumental work, which deserves a more prestigious title than merely Handbook, keys and describes all of the 300 species known from the Americas north of Mexico. It will therefore enable identification of the known pest and beneficial species, and hopefully encourage further work involving these flies in the field of plant-insect relationships. For the first two authors this book represents a synthesis of experience gained during entire career spans, supplemented by recent studies carried out by the third author, notably on the genus Anastrepha.

The book starts with an introduction which includes a mention of species of some biocontrol agent tephritids that were introduced too late for full inclusion in the work. There follows an excellent account of the adult morphology of tephritid fruit flies which is both well illustrated and applies the standardized terms first detailed in the Manual of Nearctic Diptera (J. F. McAlpine, ed., 1981). Even so, there is still
some confusion over the application of these terms as the authors use the term postalar for what I have called posterior supra-alar; and others have used post-alar for what the authors (and myself) have called the intra-alar. So much for standardization! The next section, covering biology, is very brief, but excusably so with so many fruit fly symposium volumes and multi-author works covering every worked aspect of tephritid biology, to refer to. The authors then present a review of the classifications of the family, including the first ever tabulation showing how the North American genera fit into the classification. This section is of importance to fruit fly taxonomists in all world regions as it is the first detailed account of the work that Al Norrbom has been coordinating for the last few years to try to produce a sensible globally applicable classification of the family; no mean task in a family of just 4,000 species divided among a colossal 500 genera. The following section is also worldwide in coverage as it reviews the major taxonomic literature from each zoogeographic region. The next chapter, Techniques for Study, is an excellent account of how to mount and dissect specimens, but details of collecting and rearing techniques are sadly lacking. The final introductory section is entitled About this Handbook, and it explains the scope of the keys and species accounts. This section also lists nomenclatural changes made in the Handbook, and this is a particularly good idea as I always fear Zoological Record abstractors could miss changes made within a substantial text of this sort.

The first key is to genera, as the authors very wisely make no attempt to present a key to subfamilies and tribes. This, and other keys are very clearly illustrated with figures close to the text from which they are referenced, and with a system of lettered arrows to important features. Although I found it fairly obvious what the significance of the indicated features were in almost all cases, some readers may wish they had been explained in the figure legends as well as in the keys.

In the Systematic Treatment of the Genera, the genera and species are arranged in alphabetical order. The main genera covered that include pest species are Anastrepha, Bactrocera, Ceratitis, Dacus and Rhagoletis. The key to 19 Anastrepha spp., includes the West Indian fruit fly (A.obliqua (Macquart)), Sapote fruit fly (A. serpentina (Wiedemann)) and Guava fruit fly (A. striata Schiner), all of which have distributions which abut the southern borders of the USA and represent a considerable threat to the US fruit industry. The account of Rhagoletis spp. is also likely to be well used as this includes the most important temperate fruit pests in North America, e.g. the apple maggot fly (R. pomonella (Walsh)), which has also been the subject of extensive studies of speciation processes. Many Rhagoletis spp. are also of major plant quarantine importance to Europe, and in recent years two North American species have regularly been trapped in Switzerland.

Regrettably, the account of the Bactrocera spp. that have been intercepted or trapped in the USA could have been improved by review at the manuscript stage. No Bactrocera spp. are native to the New World, although the melon fly (B. cucurbitae (Coquillett)), Oriental fruit fly (B. dorsalis (Hendel)) and solanum fruit fly (B. latifrons (Hendel)) are all established in Hawaii, and a close relative of Oriental fruit fly is also established in Suriname. All of these species, plus the Queensland fruit fly ( $B$. tryoni (Froggatt)) and two other Asian species, have been intercepted or bait-trapped in California. Fortunately none of these species have become established, but as it is important that good information on their recognition is made available, some amendments to the key are suggested here. Couplet 1 could have mentioned that the
melon fly is also separated from the other five species by having three, rather than two, stripes on the scutum. The Queensland fruit fly separates from the others by having its costal band start from the base of the wing rather than from cell sc, and then the solanum fruit fly can be separated from the Oriental fruit fly, by its yellow anepisternal stripe being triangular and contacting the yellow mark on the postpronotal lobe. Unfortunately, some of the wing photographs for this genus were based on teneral specimens, so the apical expansion of the costal band of the solanum fruit fly is not shown clearly. The authors have also chosen to perpetrate the USDA habit of calling this widespread Asian species Malaysian fruit fly, despite the fact that Malaysian agricultural entomologists voiced objections to this at a meeting I attended in Kuala Lumpur in the company of one of the authors! Naturally the Malaysians do not want to risk being singled out for fruit export bans that are equally applicable to neighboring countries.

The genera of particular importance for their inclusion of weed biocontrol agents of use in North America are Chaetorellia, Tephritis, Terellia and Urophora. All of the Urophora spp. of interest are included, although some of the distribution maps should show more Canadian records. Unfortunately the genera Chaetorellia and Terellia, both of which include species about to be released, or in some cases actually established in North America to help control some weedy Centaurea spp., are only mentioned in the introduction and are not described.

The remaining 49 genera lack species of notable economic importance, but nonetheless include a range of interesting, and in many cases very beautiful looking insects. Flies are generally underrated aesthetically, but having collected genera such as Aciurina, Gymnocarena, Paracantha and Strauzia, I can vouch for that fact that when alive, many of these North American flies have brilliant green and brown patterns across their eyes, which sparkle like jewels. A characteristic feature of the family Tephritidae is that most species have ornately patterned wings, and curiously, I suspect this has hindered proper understanding of species limits, as there has been a tendency to divide species on often trivial characters of wing pattern. While collecting in British Columbia I reared some specimens of a Tephritis sp. from flowers of an Erigeron sp. I also swept huge numbers of what I took to be a separate and consistently rather smaller species from areas where there was no Erigeron. Samples of both of these flies were sent to the authors of this Handbook for examination and both were identified as $T$. araneosa (Coquillett). Knowing the mess our European Tephritis fauna used be in as a result of the over-reliance on wing pattern, I remain skeptical of the conspecificity of those two populations. Consequently, I was very pleased that the authors mention in the introduction to the Tephritis section that "the results of future biological studies may alter our concepts at the special level," and that they also make special reference to problems associated with the concept of $T$. araneosa.

This excellent book will I hope spur North American entomologists on to make those biological studies, although the lack of a summary of existing host data appears at first sight to be a major omission. North America is the only region for which an extensive tephritid host catalogue has been published and the lack of a host list in the Handbook is therefore excusable. However, some of the host records that are quoted should have been subject to some scrutiny. For example, I find it very hard
to believe the record of $T$. araneosa from the grass Poa, since all confirmed rearings of Tephritis spp. have been from the Asteraceae.

It is regrettable that this book has clearly taken a long time between manuscript completion and publication. For example, a 1985 revision of Orellia and Terellia spp. apparently came too late to be applied to the arrangement of this 1993 publication. Similarly, recent revisions of Epochra and Paroxyna spp. could not be taken into account and I could find no mention of the recent outbreak of Mediterranean fruit fly (Ceratitis capitata (Wiedemann)) in California. Clearly, this delay would have been largely the fault of the publishers rather than the authors. Another feature which may be attributable to the publisher is that the illustrations are a little under-sized, although that is compensated for by their clarity and undoubted good quality. However, the distribution maps are not under-sized and give a very clear visual indication of the range of every species, although no distinction is made between established distribution and areas from which pest species have been eradicated.

Bearing in mind the diverse reasons for which the family Tephritidae is studied, this book should be of value in the field of plant quarantine and weed biocontrol, and it will be a major contribution to the study of North American Diptera, and in a wider context the taxonomy of Tephritidae. As I have already indicated, there is considerable scope for discovery in combining work on plant-insect relationships with the taxonomy of these delightful flies. Few works in taxonomy can rightfully claim such a wide potential audience.-Ian M. White, International Institute of Entomology, 56 Queen's Gate, London SW7 5JR, U.K.
J. New York Entomol. Soc. 102(2):283-285, 1994

Insect Pathology.-Y. Tanada and H. K. Kaya. 1993. Academic Press, San Diego. 666 pp. \$129.00.

That diseases can decimate insect populations has long been recognized, yet this subdiscipline of entomology has received relatively little attention until fairly recently. Effective biological control is in great demand; in systems where predators and parasitoids provide inadequate pest control, disease-causing organisms are now being evaluated and integrated into pest management. In fact, several microorganisms and nematodes are presently commercially available and quite a few more are in the registration process or are being developed for mass production. However, these developments demonstrate only the most readily foreseen applications of insect pathology. Research with insect pathogens has yielded major advances in entomology in the application of molecular biological methodology. For example, baculoviruses have been engineered to produce drugs for humans and crop plant varieties are protected by expression of the Bacillus thuringiensis delta-endotoxin gene. Studies of disease-causing organisms increase the basic knowledge in microbiology, protozoology, mycology, virology, and nematology as well as insect immunology. Application of computer models to patterns of disease abundance builds on generalized epidemiological theories toward developing the ability to predict disease prevalence.

This immense growth in insect pathology has been accompanied by extensive primary publication. As a rule, articles and books reviewing the new information usually focus on only one pathogen group. This same specialization is evident in recent training of insect pathologists. "Historically, students and teachers were cognizant of most, if not all, pathogen groups. Today, there are only a few scientists who fit the general insect pathologists' category, and most have specialized into subdisciplines. . ." However, specialized insect pathologists are frequently expected to answer questions and teach courses about this entire field, as well as to diagnose the cause of death of field-collected or lab-reared insects.

Insect Pathology is a unique undertaking in describing individual pathogen groups while also focussing on general principles of this entire field with emphasis on commonalities among pathogen groups. In writing this book, Tanada and Kaya planned to update Principles of Insect Pathology written by E. A. Steinhaus in 1949, the last book on general insect pathology that was not an edited volume. While the authors began this undertaking many years ago as a text, it is clear that they greatly surpassed this goal. This detailed book will be an extremely valuable resource for advanced students of insect pathology as well as specialists wanting to broaden their knowledge and general readers wanting an overview of the field. While selected individual chapters will be valuable for teaching undergraduates, the presentations on individual pathogens are frequently detailed and technical, requiring some prior knowledge of this field. In addition, the high price almost certainly excludes use of this book as an undergraduate text.

Because Insect Pathology attempts to bridge the gap from 1949-1993, an enormous amount of literature is cited, including over 185 pages of references supporting the approximately 450 pages of text presented in 16 chapters. The authors begin by truthfully stating that it was not possible to include all of the relevant literature. However, they certainly tried to include as much as possible. The 73 figures and 16 tables supporting the text are invaluable for clarification. An outline at the beginning of each chapter facilitates quick reference.

This book begins with a brief introduction and history of insect pathology and proceeds with a chapter on the microorganisms associated with insects that do not cause disease. While treatment of this subject is not expected under the umbrella of insect pathology, it has traditionally been covered by this discipline. Amicrobial diseases are discussed next along with an introduction to what makes an organism a pathogen, including basic terminology and principles of insect pathology.

The next block of 10 chapters describes pathogenic bacteria, viruses, fungi, protozoa, and nematodes and comprises the majority of the text. Treatments of these different groups are frequently organized somewhat similarly such that comparisons between groups can be more easily made. For example, subheadings for most groups denote sections on pathogenesis and signs and symptoms of diseases. Of course, these chapters cannot completely cover the similarities among the pathogen groups because of the diverse nature of these groups, with related research developments that are not parallel. The four chapters on viruses are especially conspicuous in having a level of detail exceeding the treatments of other pathogen groups, certainly illustrating the years of experience and expertise of the senior author.

The chapter on host resistance includes discussions of the diversity of levels of resistance, including a basic description of classes of hemocytes to supplement the
section on cellular immunity. Concluding chapters compare microbial control and epizootiology of different pathogen groups, providing case studies of different pathogens and ecosystems as examples.

While insect pathologists may criticize particular individual sections of this book as lacking in depth, these authors clearly meant to produce an integrative overview of this subject. It would be difficult for a single volume such as this to include more detailed presentations from throughout this broad field and still maintain an emphasis on parallels between different groups.

This book is a valuable asset to the literature in its up-to-date synthetic treatment of this diverse field. Such a comparative endeavor is most likely to succeed with a consistency in presentation that is only possible with one to a few authors. Tanada and Kaya should be applauded for their tenacity in single-handedly struggling with such an immense subject, an endeavor that is seldom attempted in recent years, i.e., see the abundance of edited volumes in this field. Such a detailed and diverse treatment could only be possible with expertise gained by many years of working and teaching in many aspects of this field, as have both of these authors. This book is long overdue and will certainly help to broaden the knowledge of pathologists in this increasingly specialized field.-Ann E. Hajek, Boyce Thompson Institute, Tower Road, Ithaca, New York 14853-1801.

## INSTRUCTIONS TO AUTHORS

The Journal of the New York Entomological Society publishes original research resulting from the study of insects and related taxa. Research that contributes information on taxonomy, classification, phylogeny, biogeography, behavior, natural history, or related fields will be considered for publication. 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.

Manuscripts should be submitted in triplicate to: Dr. James M. Carpenter, Editor, Journal of the New York Entomological Society, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. Contributions must be written in English, double-spaced (including references, tables, captions, etc.) and prepared in the format of a recent issue of the Journal. Manuscripts of any length will be considered for publication. Longer papers will be printed as articles, shorter ones as "scientific notes." Book reviews will be solicited by the Book Review Editor.

Longer manuscripts intended for submission as articles should be accompanied by a brief abstract. Footnotes should be avoided. Tables should be prepared as separate pages; they should be kept to a minimum because of the high cost of typesetting, but may be submitted as photographically reproducible material (see below). The list of references is headed "Literature Cited" and should follow the format indicated in the CBE Style Manual or as found in a recent issue of the Journal. Manuscripts should be printed in roman, bold roman, or underlined roman or bold roman to conform to journal typesetting style. Manuscripts should not contain any italic fonts. Manuscripts containing cladistic analyses should be accompanied by a copy of the data matrix on diskette for verification of the calculations.
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# Journal of the New York Entomological Society 

## CONTENTS

| Recognition of the West Asian Anchomenus kurnakovi and A. punctibasis (Co- |
| :--- |
| leoptera: Carabidae: Platynini) and Miocene evolution of the Mediterranean |
| and Paratethys Seas |
| James K. Liebherr |
| A new genus and four new species of Colpurini (Hemiptera: Heteroptera: Corei- |
| $\begin{array}{l}\text { 127 } \\ \text { dae) from New Guinea } \\ \text { Harry Brailovsky }\end{array}$ |
| $142-153$ |

Hydroptilidae (Trichoptera) of Costa Rica and the Neotropics: Systematics of the
genus Byrsopteryx Flint (Stactobiini)
Steven C. Harris and Ralph W. Holzenthal
154-192
A generic conspectus of the tribe Procleticini Pennington (Heteroptera, Pentatomidae), with the description of Parodmalea rubella, new genus and species
D. A. Rider

193-221
West Indian Coccinellidae V (Coleoptera): A review of Coccidulini and additions
to Psorolyma Sicard
Robert D. Gordon
$\begin{array}{lrl}\text { West Indian Coccinellidae VI (Coleoptera): new genera and species of Sticholoti- } \\ \text { dini and a cladistic analysis of included genera } & \text { Robert D. Gordon } & \text { 232-241 }\end{array}$
$\begin{aligned} & \text { The stridulatory mechanism of Nerthra Say, a new species, and synonymy (Het- } \\ & \text { eroptera: Gelastocoridae) }\end{aligned} \quad$ John T. Polhemus and Per Lindskog 242-248
A new species of Octotoma Chevrolat, 1837, from Guatemala (Coleoptera:
Chrysomelidae, Hispinae)
C. L. Staines
Pemphigus obesinymphae, a new American aphid species with defenders and
swollen nymphs (Homoptera: Aphidoidea: Pemphigidae)
Shigeyuki Aoki and Nancy A. Moran
251-260
A new species of Ambrysus Stål from Ash Meadows, Nevada (Heteroptera: Nau-
coridae)
John T. Polhemus and Dan A. Polhemus 261-265
Notes and Comments
Vibrational signals associated with mating behavior in the treehopper, Enchenopa binotata Say (Hemiptera: Homoptera: Membracidae) Randy E. Hunt

266-270
Stridulatory mechanisms in aquatic and semiaquatic Heteroptera
John T. Polhemus
270-274
A replacement name for Myrmecomiris Polhemus and Razafimahatratra (Het-
eroptera: Miridae)
Dan A. Polhemus

## Book Reviews

Beetle Larvae of the World: Interactive Identification and Information Retrieval for Families and Subfamilies

Joseph V. McHugh
276-280
Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico
Ian M. White
280-283
Insect Pathology
Ann E. Hajek 283-285
JS67 12 JULY 1994 No. 3

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Meetings of the Society are held on the third Tuesday of each month (except June through September) at 7 p.m. in the American Museum of Natural History, Central Park West at 79th Street, New York, New York.

Mailed March 22, 1995

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# ABSENCE OF KIN DISCRIMINATION BEHAVIOR IN A SOLDIER-PRODUCING APHID, CERATOVACUNA JAPONICA (HEMIPTERA: PEMPHIGIDAE; CERATAPHIDINI) 

Norman F. Carlin, David S. Gladstein, Andrew J. Berry, and Naomi E. Pierce*<br>119 Governor Winthrop R., Somerville, Massachusetts 02145;<br>College of Computer Science, Northeastern University, Boston, Massachusetts 02115 ; and<br>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138


#### Abstract

Certain aphid species produce sterile soldiers, morphologically and behaviorally specialized individuals that defend fertile colony members, some or all of which are clonemates. If the soldier morph is maintained by inclusive fitness advantages, its altruism should preferentially benefit relatives, suggesting a potential role for kin discrimination. We performed a field experiment on spatial segregation and two laboratory experiments on agonistic behavior among non-soldiers and by soldiers of the cerataphidine aphid, Ceratovacuna japonica. For the test of spatial segregation, we introduce a new method of nearest-neighbor analysis, by constructing a minimum spanning tree from the map of individual locations and comparing the numbers of within-group and between-group connections. The results provide no evidence of kin recognition abilities in this species. Members of different clones showed no tendency to segregate spatially, nor to direct displacement attempts against non-kin when competing for feeding sites. Soldiers were indiscriminately aggressive toward early instar reproductives from their own and other colonies. We discuss the implications of these findings for several evolutionary hypotheses on the maintenance of the soldier morph in aphids.


The discovery of sterile aphid soldiers (Aoki, 1977) has been widely interpreted as confirming a prediction of inclusive fitness theory, that altruism can evolve within clones of cyclically parthenogenetic organisms (Dawkins, 1979; Aoki, 1987; Hamilton, 1987; Ito, 1989). Soldiers are first or second instar individuals which are morphologically and behaviorally specialized for colony defense and which, in failing to molt to adulthood, do not reproduce. Soldier morphs have evolved independently at least four times among pemphigid aphids, and soldier-like behavior by monomorphic first instars, which do become reproductive adults, also occurs in some species (Aoki and Kurosu, 1987; Kurosu and Aoki, 1988; Moran, 1993). Attacks by soldiers and monomorphic defenders on vertebrates and the eggs and larvae of predatory insects have been documented in a number of studies (Aoki, 1979; Ohara, 1985; Aoki and Kurosu, 1987; Kurosu and Aoki, 1988; Foster, 1990). If the colony originated from one parthenogenetic foundress, soldiers protecting fertile colony members would promote the reproduction of their clone, a role analogous to that of somatic cells in a metazoan body (Dawkins, 1979; Hamilton, 1987).

However, were some females to join a colony but produce fewer or no soldiers, the "cheaters" could enjoy enhanced reproductive success at the expense of the soldier-producers (Aoki, 1980; Hamilton, 1987). The proportion of soldiers is highly labile both between colonies and, over time, within colonies (Sunose et al., 1991;
*to whom correspondence should be addressed

Sakata et al., 1991), suggesting that there may be some variation in soldier-producing propensity, which could facilitate the generation of cheating mutants. Ito (1989), summarizing suggestions of previous authors (e.g. Aoki, 1987; Hamilton, 1987), offered three hypotheses for the evolution and maintenance of soldier production under these circumstances: (1) soldiers recognize and expel unrelated genotypes, preserving clonal integrity; (2) dispersing females join established colonies so infrequently that genetic mixing is unlikely; or (3) predation pressure requires the maintenance of a certain proportion of soldiers even if colonies are genetically diverse, while failure to produce soldiers decreases colony fitness. The experiments reported here were designed to test an expanded version of the kin recognition hypothesis. Kin discrimination by soldiers, and/or by reproductives, could preserve effective clonal integrity by the exclusion of most or all foreign intruders, as in Ito's hypothesis 1 (henceforth referred to as hypothesis 1a). Alternatively, discrimination could enable soldiers preferentially to defend clonemates within a genetically diverse colony (hypothesis 1 lb . E.g., if the usually sedentary reproductives form spatially segregated, clonal subgroups, kin recognition could enable the mobile soldiers to remain in the vicinity of their clonemates.

In addition, apparently agonistic interactions within colonies have been observed in the form of "butting" behavior, by which aphids attempt to displace fellow colony members from feeding sites (Aoki et al., 1981; Aoki and Kurosu, 1985). Aoki (1987) reported intracolonial butting in all species studied in the tribe Cerataphidini, including soldier-producing and monomorphic species, and speculated that the defensive behavior and frontal horns of soldiers derived from butting by monomorphic precursors. Noting that conflict is unexpected within pure clones, Aoki suggested that such colonies might indeed be genetically diverse, in contradiction to hypotheses (1a) and (2), but consistent with (1b) or (3). (Other interpretations of butting are possible; see Discussion.) Unfortunately, no data on the genetic composition of colonies are yet available for any soldier-producing aphid species. However, the hypothesis that kin discrimination is used to direct butting toward non-clonemates can be tested.

Ceratovacuna japonica (Hemiptera: Pemphigidae; Cerataphidini) produces "pseu-doscorpion-like" first instar soldiers, with prolonged, sharp frontal horns and thickened, grasping forelegs (Aoki, 1977, 1987). Dense clusters of these woolly aphids are commonly found on the underside of bamboo grass leaves (Pleioblastus spp.), the secondary host (Aoki and Kurosu, 1991). For the purpose of this study, a "colony" is functionally defined as an aggregation of aphids on one leaf, which can benefit from defense by the soldiers present on that leaf. The inhabitants of multiple leaves on the same or neighboring plants may constitute one genetic population, however. Production of an alate sexual phase, migration to a primary host and gall formation are uncommon in this species; in fact, its gall generation and primary host (Styrax japonica) have been discovered only recently (Aoki and Kurosu, 1991). Most colonies are founded asexually by non-soldier first instars, dispersing on the wind to new plants (Pierce and Berry, unpubl.). In dense populations, over the lifetimes of colonies, it seems possible that a dispersing female may arrive on an already occupied host plant, but the frequency of this event remains unknown.

We tested C. japonica aphids for recognition of colonymates and putative clonemates in the contexts of spatial segregation, butting and soldier aggression. Incipient colonies separated by large distances were used in the first two experiments because
they were more likely to be pure clones, still comprised only of offspring of the first female to arrive on the plant. Since incipient colonies contain few soldiers, larger colonies provided soldiers for the third experiment, though an unknown number of subsequently arriving females may have contributed to these colonies. Were these aphids capable of recognizing kin as required by hypotheses (la) or (1b), we expected to observe discrimination against members of foreign colonies in at least one of these three behavioral contexts.

## METHODS

Experiment 1-Spatial segregation. Experiments were conducted in the laboratory of Dr. S. Aoki and in stands of bamboo grass (Pleioblastus chino) in the vicinity of Rissho University, Kumagaya, Saitama Prefecture, Japan, in July 1988. In all experiments, C. japonica colonies assumed to be unrelated were collected from sites at least 1 km apart. For experiment 1 , the test of spatial segregation, 56 incipient colonies were collected, containing either one adult aphid with a group of early instars ( $22 \pm 11$ each, mean $\pm \mathrm{SD}, \mathrm{N}=16$ colonies), or a group of early instars without an adult ( $20 \pm 12$ each, $N=40$ ). Incipient colonies containing one adult female were presumably all offspring of that adult. Of those without an adult, most were probably the offspring of one recently-deceased foundress, since it seems unlikely that large numbers of independently wind-dispersed individuals would arrive synchronously on one leaf. The results obtained with both types of colony did not differ (see Tables 1, 2). Most incipient colonies do not contain soldiers; two of this sample of 56 included one soldier each, and one included two soldiers.

Pairs of colonies from different sites, containing approximately equal numbers of individuals, were marked with different colors of fluorescent dust (Crumpacker, 1974), which is readily absorbed by the white waxy secretions that coat these woolly aphids. Individuals were placed one by one, alternating the colony of origin, onto a marked spot on the upper surface of an unoccupied bamboo grass leaf in the field. The aphids quickly moved to the underside of the leaf, allowing the placement of the next individual on the same spot. After 24 hours, the leaf was cut and the positions of all marked individuals remaining on its lower surface were recorded.

To test for non-randomness in the distributions of the two groups, we employed a new method of nearest neighbor analysis, based on the construction of a minimum spanning tree between observed data points. Pielou's (1961) contingency table procedure has been the standard method for analysis of nearest neighbor frequencies. However, Meagher and Burdick (1980) demonstrated that nearest neighbor pairs are often not independent, violating the assumption of the $\chi^{2}$ test. If individual A is B 's nearest neighbor, B is likely to be A's, so some pairs are counted twice. Meagher and Burdick proposed an alternative significance test, which requires extensive computer simulation of randomized data sets, but stated that a simpler test would be preferable. We introduce here a simple test of spatial association that can be carried out manually.

Given a map of the locations of N individuals belonging to groups 1 through k , N -1 point-to-point connections can be drawn so that there is a path between any two points, and the summed length of all connections is minimized. This construction, a minimum spanning tree, contains all nearest neighbor pairs if the interpoint distances are unique (Cheriton and Tarjan, 1976). The connections between points are independent, in that reciprocal pairs cannot occur. The procedure for constructing a

Table 1. Spatial aggregation in pairs of C. japonica colonies, by minimum spanning tree method for nearest-neighbor analysis, described in the text. Observed and expected numbers of nearest-neighbor connections between members of the same colony are compared by $\chi^{2}$ test; n.s. $=$ not significant at $P>0.05$. Colonies are numbered arbitrarily; those marked with an asterisk contained an adult.

| Replicate | \# Individuals |  | \# Same-colony neighbors |  | Significance |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Col. 1 | Col. 2 | Obs. | Exp. |  |
| 1 | 11 | 5* | 8 | 8.1 | n.s. |
| 2 | 20* | 7 | 15 | 15.6 | n.s. |
| 3 | 7 | 17 | 15 | 13.1 | n.s. |
| 4 | 20* | 10* | 18 | 15.7 | n.s. |
| 5 | 7 | 17 | 12 | 13.1 | n.s. |
| 6 | 6 | 8 | 5 | 6.1 | n.s. |
| 7 | 5 | 9 | 5 | 6.6 | n.s. |
| 8 | 14 | 13 | 13 | 12.5 | n.s. |
| 9 | 22* | 19 | 24 | 19.6 | n.s. |
| 10 | 16* | 29* | 26 | 23.4 | n.s. |
| 11 | 9 | 4 | 6 | 6.5 | n.s. |
| 12 | 34 | 31 | 33 | 31.6 | n.s. |
| 13 | 6 | 9 | 10 | 6.8 | n.s. |
| 14 | 6 | 28 | 24 | 23.1 | n.s. |
| 15 | 5* | 21 | 21 | 16.9 | n.s. |
| 16 | 3 | 24 | 22 | 20.7 | n.s. |
| 17 | 12 | 24 | 18 | 19.0 | n.s. |
| 18 | 10* | 15* | 12 | 12.0 | n.s. |

minimum spanning tree for a given data set is as follows: (1) Pick any point to be first in the tree; (2) Find the point not yet in the tree which is closest to any point in the tree, and connect it to the latter; (3) Repeat step 2 until all points are included (Even, 1979). The frequencies of within-group and between-group connections can be arranged in a contingency table. Since the order of the connected points is unimportant, we adopt the convention that the table be lower-diagonal; i.e., the observed frequency $f_{i, j}$ is the number of $(i, j)$ and $(j, i)$ connections. Letting $n_{i}$ denote the number of members of group $i$, the expected frequencies are $e_{i, j}=n_{i}\left(n_{i}-1\right) / N$ for $i=j$; and $\mathrm{e}_{\mathrm{i}, \mathrm{j}}=2 \mathrm{n}_{\mathrm{i}} \mathrm{n}_{\mathrm{j}} / \mathrm{N}$ for $\mathrm{i}>\mathrm{j}$. For the $\chi^{2}$ test, the table has $\mathrm{k}(\mathrm{k}-1) / 2$ degrees of freedom. This method has been tested by Monte Carlo simulation for sample sizes between 20 and 100, and performs as expected (Gladstein, unpubl.).
Experiment 2-Butting behavior. To test for discrimination in butting, 20 incipient colonies were collected. Nine of the colonies included one adult and $16 \pm 8$ early instars each, 11 colonies without an adult contained $17 \pm 10$ early instars each, and 10 also included one or two soldiers. (Incipient colonies with soldiers were selected for this experiment, since potential competition for feeding sites by non-reproductives is of particular interest.) Sections of leaves on which the aphids were feeding were excised and taken to the laboratory, where pairs of colonies from different sites were color-marked with fluorescent dust and their leaf sections fixed upside down in a petri dish, with the margins of the two groups abutting. After several hours, as the

Table 2. Agonistic interactions (butting) between pairs of C. japonica colonies. Observed and expected numbers of interactions between individuals from different colonies are compared by $\chi^{2}$ test; n.s. $=$ not significant at $P>0.05$. In replicates marked with an asterisk, one colony contained an adult; in those marked with two asterisks, each contained an adult.

|  | Total \# <br> Replicate | \# Betw.-colony interactions |  |  |
| :---: | :---: | :---: | :---: | :--- |
|  |  | Exp. | Significance |  |
| 1 | 121 | 49 | 64 | $P<0.005$ |
| $2^{*}$ | 133 | 58 | 58 | n.s. |
| $3^{*}$ | 52 | 24 | 23 | n.s. |
| $4^{*}$ | 86 | 50 | 45 | n.s. |
| $5^{*}$ | 106 | 47 | 50 | n.s. |
| 6 | 202 | 96 | 90 | n.s. |
| $7^{* *}$ | 70 | 23 | 28 | n.s. |
| $8^{*}$ | 170 | 63 | 62 | n.s. |
| 9 | 24 | 11 | 11 | n.s. |
| $10^{* *}$ | 53 | 24 | 27 | n.s. |

cut leaves began to dry, individual aphids from both colonies ceased feeding and began to wander among those still feeding.

Butting behavior, in which a mobile individual thrusts its head against a feeding individual in an apparent attempt to displace it from the feeding site (described by Aoki and Kurosu, 1985), was recorded in a series of 1 hour sessions, totalling 19 hours. Most colony pairs were observed for 2 hours, but pairs 2 and 9 were observed for only 1 hour, after which no aphids were feeding and butting ceased; and pair 1 was observed for 3 hours. We recorded the colony of origin, morph and size (adult or early instar; no late instar juveniles were present) of the interactants, and success or failure in displacing the victim from its feeding site. Single butts were uncommon; most interactions consisted of several or many separate thrusts. Repeated thrusts against the same individual were scored as one interaction unless the attacker walked off, then returned to butt its previous victim again. To test the null hypothesis that butting is independent of colony membership, the observed scores of interactions between and within groups were arranged in a contingency table, and the values expected for each cell were obtained by cross-multiplying the marginal totals:

$$
\text { Expected [i butts } \mathrm{j}]=\frac{\text { observed [i butts] } \times \text { observed }[\mathrm{j} \text { is butted] }}{\mathrm{n}},
$$

where n is the total number of interactions per colony pair. Expected and observed values in the $2 \times 2$ tables were compared by $\chi_{1}{ }^{2}$ test. For brevity of reporting, only the sums of between-colony interactions are given in Table 2; for two colonies, A and B , this is equal to

$$
\frac{[\mathrm{A} \text { butts } \mathrm{B}]+[\mathrm{B} \text { butts } \mathrm{A}]}{\mathrm{n}} .
$$

Experiment 3-Soldier agonistic behavior. To examine the agonistic responses of soldiers to early instar reproductives, soldiers were obtained from large colonies
containing hundreds of aphids of all stages, because incipient colonies contain few soldiers. Depending on the frequency with which females arrive at already occupied plants, the soldier source colonies may or may not have been pure clones. From each of 27 colonies, a group of soldiers ( $5.7 \pm 3.6$ per colony) was collected and placed on a leaf, fixed upside down in a petri dish in the laboratory. The soldiers walked actively on the leaf surface, often with their thickened forelegs raised in an apparently threatening posture. In preliminary tests, other conspecific aphids were placed on the leaf and observed as the soldiers encountered them. In this context, soldiers failed to exhibit any detectable behavioral response to over 50 conspecifics, including soldiers and non-soldiers from their own and other colonies. However, soldiers did respond to early instars held before them in forceps, clasping the aphids with their forelegs and jabbing with their frontal horns. Each soldier was presented with two early instar reproductives held in forceps, one from its own colony and the other from a different site. Responses were recorded blindly; i.e., the origin of the soldiers was unknown to the observer. The order of presentation of the two early instars was alternated, and the forceps were washed between presentations.

## RESULTS

Experiment 1-Spatial segregation. Many of the marked aphids disappeared overnight, but sufficient numbers for analysis were recorded in 18 of the 28 replicates, for which the mean number of individuals recovered per colony was $14.0 \pm 8.5$. To compensate for low recovery rates in some colonies, we combined the 1-1 and 2-2 cells of the contingency table to form one "same-colony" cell, treating the 1-2 cell as the "different-colony" cell for the $\chi^{2}$ test. In 4 replicates, all individuals from one or both colonies were gone, while in another 6 , the numbers remaining generated expected values of less than 5 .

The numbers of nearest neighbor pairs composed of aphids from the same and different colonies did not differ significantly in any replicate (Table 1). Though small sample sizes may have weakened the power of some significance tests, neither was there an overall, insignificant trend across replicates. In 10 replicates, the expected number of same-colony nearest neighbors was less than observed; in 7 expected values exceeded observed, with 1 tie ( $P=0.63$, sign test). Members of incipient colonies containing an adult (indicated with an asterisk in Table 1), with a greater certainty of clonal composition, exhibited no greater tendency to aggregate than members of colonies without an adult. Thus there was no evidence of kin-biased spatial segregation.
Experiment 2-Butting behavior. Observation of butting between and within incipient colonies yielded no evidence of agonistic discrimination (Table 2). In 9 out of 10 colony pairs, including 7 in which one or both colonies contained an adult, there was no significant difference between the numbers of butts directed toward colonymates and non-colonymates. Again the negative result could not be explained by sample limitations. With the expected number of between-colony interactions exceeding observed in 4 replicates, observed values exceeded expected in 4 , and 2 ties, there was no insignificant trend ( $P=1.0$, sign test). The rate of butting tended to increase in all colonies in the second hour of observation, as the leaves dried out and increasing numbers of aphids sought better feeding sites. Separate analyses of
data from the first and second hours for each colony revealed no differences in bias, however.

In replicate 1 , butting was observed significantly less than expected between colonies; that is, putative kin were butted preferentially. Since any individual test in a sufficiently large statistical table may yield significance by chance, the table-wide probability of significant outcomes should also be calculated (Rice, 1989). The tablewide probability of this result is less than 0.05 . The first pair of colonies was observed for 3 hours, while all other pairs were observed for 1 or 2 , but the result is significant even when only the first 2 hours of data on replicate 1 , totalling 49 interactions, are counted: 15 between-colony butts observed, 24 expected, $P<0.01$, $\chi^{2}$. However, counting only the first 2 hours, the table-wide probability of a chance result exceeds 0.05 .

Of the total of 1,017 butting interactions recorded, $92 \%$ were between early instars. However, though few in number, the adults and soldiers also occasionally participated, initiating $3 \%$ of butts and receiving $5 \%$. The results of the above analysis were not altered by excluding interactions involving adults and soldiers, while this subset of data was too small to test separately for kinship bias. It is worth emphasizing, though, that early instars did sometimes butt their own putative clonemothers ( $\mathrm{N}=$ 15 occurrences in the entire data set), as well as adults from other colonies ( $\mathrm{N}=20$ ); adults butted their own putative offspring ( $\mathrm{N}=9$, vs. 5 for non-colonymates); and sterile soldiers butted their own putative fertile clonemates ( $\mathrm{N}=7$, vs. 10 for noncolonymates). Soldiers used their heads when butting, in the same manner as the fertile morphs, never using their forelegs to clasp opponents as observed in experiment 3. Contrary to hypothesis (1a), the soldiers made no attempt to exclude foreigners by butting, clasping or otherwise attacking as they moved among members of both colonies. They ignored other soldiers entirely, though a soldier once butted a foreign adult.

Following many, but not all, successful displacements the aggressor began to feed at the vacated site. However, most aggressors did not succeed in displacing their victims. Of the 94 ( $9 \%$ ) successful displacements, 48 were of colonymates, 46 of noncolonymates, while 524 failed butts were directed toward colonymates, 399 toward non-colonymates ( $P>0.05, \chi^{2}$ ). As Aoki and Kurosu (1985) reported, larger individuals are more successful at displacing smaller ones. Thus adults displaced early instars in 8 of 14 attempts, while an early instar succeeded in moving an adult only once out of 35 attempts. The poor success rate of butting was not the result of elaborate defense behavior. The recipients of butting often rotated or flattened their bodies, but infrequently raised their abdomens in the "headstands" that Aoki and Kurosu (1985) observed in Astegopteryx bambucifoliae. On occasion the aggressor and opponent locked horns and rotated around the latter. Very rarely the recipient, its mouthparts still inserted in the plant, butted the aggressor in return. No injuries were observed in any of these interactions.
Experiment 3-Soldier agonistic behavior. When presented with early instar reproductives from their own and other colonies, held in forceps, the sample of 156 soldiers failed to attack aliens significantly more than colonymates. Ninety-nine soldiers aggressively clasped both of the offered early instars between their thickened forelegs, and 22 ignored both. Of the 35 soldiers which responded asymmetrically, 18 clasped the aphid from an alien colony but not the one from their own, and 17
clasped the one from their own colony but not the alien ( $P>0.05$, binomial test). Detection of the early instars was not based on touch or contact chemoreception, since the soldiers raised their forelimbs and began to make clasping motions before contact. They may react to visual stimuli and/or to alarm pheromones contained in the dark brown fluid which these aphids release from their siphunculi when held. Defensive first instars of a monomorphic cerataphidine, Ceratovacuna lanigera are known to exhibit an aggressive response to alarm pheromones (Arakaki, 1989).

## DISCUSSION

## Absence of kin discrimination

Kin recognition could enable soldier or reproductive aphids to expel or avoid unrelated conspecifics, preserving colony clonality (hypothesis la); or it could enable soldiers to defend their clonemates discriminatingly within genetically diverse colonies that are compartmentalized into pure clone subgroups (hypothesis 1b). Our results appear to exclude both these hypotheses for Ceratovacuna japonica. Soldiers did not discriminate against foreign early instar reproductives which, dispersed by wind from other colonies, are the most probable intruders. Members of different clones showed no tendency to segregate spatially, or to butt non-kin preferentially in competition for feeding sites, which would promote the spatial separation of genotypes. In experiments on three other aphid species, Pemphigus spyrothecae (Foster, 1990), Ceratoglyphina styraciola (Aoki et al., 1991; Aoki and Kurosu, 1992) and Pseudoregma bambucicola (Sakata et al., 1991), soldiers also failed to direct agonistic behavior preferentially against non-colonymates. Kin-biased spatial segregation and butting have not been tested in other soldier-producing species.

Studies of kin recognition must always consider the essential caveat that failure to discriminate cannot prove failure to recognize (Waldman et al., 1988). Any experimental assay of recognition capabilities (except perhaps an electrophysiological one) requires measuring an observable behavioral response, but behavioral responses are often context-dependent. Aphids may spatially segregate by kinship under normal circumstances, but not when suddenly transferred to a new leaf; soldiers may normally exclude non-kin, but attack anything thrust at them with forceps. (Note, however, that this admittedly crude assay was necessitated by the soldiers' failure to respond at all in less contrived encounters.) However, we can conclude that there is no evidence of a simple behavioral mechanism insuring the genetic integrity of the colony, or of spatial subgroups within the colony.

The fact that the sexual phase of the life cycle has been largely suppressed in $C$. japonica might make kin recognition impracticable for this species. Depending on the rates of mutation, sexual reproduction and long-distance dispersal, entire local populations could be effectively pure clones. In that case, there would be no differential inclusive fitness advantage for discriminatory behavior, and insufficient phenotypic variation to permit recognition. (This situation would not be unique to $C$. japonica; some other soldier-producing aphids are also known to produce sexual generations infrequently [Aoki, pers. comm.].) Phenotypic cues acquired from the environment might still vary between colonies as in some, perhaps all, species of social Hymenoptera (Carlin, 1989). Acquired cues presumably would not suffice for
within-colony discrimination, however, given the common chemical environment of cohabiting clones.

We assume that all or most of the incipient colonies used in experiments 1 and 2 were pure clones, and that the absence of significant bias was the result of random interaction. Since the genetic diversity of colonies is undetermined, we cannot exclude the alternative possibility that one incipient colony might contain multiple genotypes, yielding the same results if individuals avoided or butted both unrelated members of their own colony and foreigners, and aggregated with or refrained from butting genuine clonemates. It seems highly unlikely, however, that every one of the newlyfounded colonies already contained the offspring of multiple females. Rather, we would expect some colonies (those which were genetically mixed) to exhibit no discrimination, while others (still pure clones) would display quite strong discrimination. Instead, the lack of significant results was highly consistent across replicates. The sole significantly non-random result, in replicate 1 of the butting experiment, cannot be explained by such within-colony nepotism, since kin were butted more often than non-kin.

## Butting behavior

In the absence of evidence for discriminatory butting between clones, other explanations for this behavior must be considered. Ordinarily butting is a response to desiccation of the leaves on which the aphids feed, and occurs in overpopulated, aging colonies rather than in tiny, incipient ones. Some individuals give up feeding at unprofitable sites and butt others that are still feeding, in an apparent attempt to displace them; if successful, the aggressor often begins to feed at the vacated site. If colonies become genetically diverse as additional females arrive on occupied plants, such that a colony that has attained sufficient size to damage its host is so heterogeneous that any neighbor is unlikely to be a clonemate, then selection should favor indiscriminate aggression. Reeve (1989) showed that universal intolerance can be selected for even when groups are usually composed of close kin, if the fitness advantage of discriminating against the occasional non-relative is sufficiently higher than the cost of incorrectly rejecting kin. In C. japonica, butting of clonemates may represent false-negative errors resulting from a highly restrictive acceptance threshold.

Indiscriminate butting does not necessarily require that colonies are genetically diverse, however. Alternatively, immigration may be negligible, such that large colonies on failing host plants are still pure or nearly pure clones. Inclusive fitness theory does allow competition among close relatives, even clonemates, if on balance the benefit to the genotype exceeds the cost (Hamilton, 1964). This is clearly the case when already-reproducing adult aphids displace early instars, which are only potential reproducers. Generally, early instars should value their $100 \%$ related, now reproductive mother much more highly than themselves, but hungry young aphids might attempt to displace their sated mother, as well as well-fed clonemates. More problematic is our observation that sterile soldiers sometimes butt their own fertile clonemates. (Soldiers butting reproductives have also been reported in Pseudoregma alexanderi [Aoki et al., 1981].) Still, the soldier's life does have a protective value for its clonemates, and a sated reproductive might occasionally give way to a starving soldier, depending on the cost-benefit ratio.

As a further alternative hypothesis, butting might represent cooperative communication, rather than competition, among members of a pure clone. Desiccation of the host plant represents an emergency condition, to which the colony eventually responds by dispersal (Pierce, Berry and Carlin, in prep.). Butting could constitute a means of spreading information about the imminent decline of the host, facilitating the successful exodus of clonemates. Such information exchange would optimize the allocation of resources: smaller individuals are most easily displaced, and these have the greatest chance of success in wind dispersal. Large adults would do better to monopolize the dwindling food supply and produce a final crop of dispersing first instars. The low probability of successful displacement and the persistence of some unsuccessful "aggressors" may suggest a competitive interaction resisted by the victim, rather than ritualized communication (Aoki, 1987). Nevertheless, the energetic cost of butting could be sufficiently small to be consistent with this scenario.

## Evolutionary hypotheses

Our finding that $C$. japonica aphids exhibit no evidence of kin discrimination behavior, in several important contexts in which such behavior is expected, appears to exclude hypotheses (1a) and (1b). Given that the existence of intracolonial butting cannot itself be considered evidence of genetic diversity, the other two possibilities summarized by Ito (1989) remain open: the soldier morph could be maintained by a dispersal pattern tending to preserve clonal integrity (hypothesis 2 ), or by high predation pressure on mixed colonies (hypothesis 3). Though soldier aphids are often cited as a paradigmatic product of inclusive fitness (e.g., Trivers, 1985), it is worth noting that hypothesis (3) might well operate by group, not kin, selection. Soldier production would be evolutionarily stable in multi-clone colonies only if each "cheater" female suffered an immediate and direct fitness cost from failing to contribute to the collective defense. Females that joined colonies but did not produce soldiers would prosper temporarily, but ultimately suffer the eradication of their group. This is a straightforward structured-deme model of group selection (Wilson, 1980) in which the groups are composed of multiple clones, rather than unrelated individuals. The fact that groups happen to consist of multiple clones should make no difference, however. The great efficiency with which predatory insects can devastate entire aphid colonies (Pierce, Berry, and Carlin in prep.) could provide the requisite high rate of group extinction as well as the need for defense. Since cheaters are expected to increase locally, this hypothesis yields the experimentally testable prediction that soldier production will soon decline or cease in an aphid population that is shielded from predators.

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# CLADISTIC PLACEMENT OF THE SUBANTARCTIC GENUS HaVERSIELLA (COLEOPTERA: CURCULIONIDAE) 

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#### Abstract

Haversiella Schweiger is comprised of a single species, H. albolimbata (Champion), which is recognized by body vestiture lacking setae, maxillary mala lacking teeth, subcircular pronotum, postocular lobes absent, scutellum very reduced, elongate elytra, tibiae lacking spurs, and reduced plate of female sternum 8. This genus belongs in the tribe Rhytirrhinini and is the sister genus to Neopachytychius Hustache. Both genera are part of a larger monophyletic group, that includes Palaechtus Waterhouse and related genera from Tristan da Cunha-Gough, and the American genera Listronotus Jekel and Lixellus LeConte. Haversiella albolimbata is distributed on the Falkland Islands and the Magellanic moorland of southern Argentina and Chile.


Haversiella Schweiger is a little-known monotypic genus of weevils, originally described by Champion (1918) as Haversia. Ringuelet (1955) noted that this generic name was preoccupied by Haversia Roewer, 1913 (Opiliones) and Schweiger (1958) proposed the name Haversiella to replace it. Earlier authors considered that its only described species, H. albolimbata (Champion), was endemic to the Falkland Islands (Champion, 1918; Ringuelet, 1955; Schweiger, 1958). Kuschel (1960) later reported it from Navarino Island (Chile). Recently, while sorting miscellaneous weevils at the National Museum of Natural History, Washington, I discovered more specimens of this species, collected in Tierra del Fuego (Argentina). The objectives of this paper are to determine the cladistic placement of Haversiella, to comment on its geographic distribution, and to redescribe and illustrate its single species.

Specimens were provided by the Natural History Museum, London, United Kingdom (BMNH); Museo Nacional de Historia Natural, Santiago, Chile (MHNS); and National Museum of Natural History, Washington D.C., U.S.A. (USNM). Measurements were made with an ocular micrometer in a stereoscopic microscope. Total length was measured dorsally, along the midline, from the elytral apex to the fore margin of pronotum. Drawings were made with a camera lucida attached to the stereoscopic microscope.

## Haversiella Schweiger <br> Type species Haversia albolimbata Champion (original designation)

Haversia Champion, 1918:185 (not Roewer, 1913); Klima, 1934:144 (cat.); Blackwelder, 1947:826 (list).
Haversiella Schweiger, 1958:42 (replacement name for Haversia Champion); Kuschel, 1960:547 (biog.), 1971:28 (biog.); Wibmer and O’Brien, 1986:120 (checklist).
Diagnosis. Haversiella is recognized by its body vestiture lacking setae, maxillary mala lacking teeth, pronotum subcircular, postocular lobes absent, scutellum very reduced, elytra elongate, tibiae lacking spurs, and plate of female sternum 8 reduced.


Figs. 1-8. Haversiella albolimbata (Champion). 1, habitus (dorsal); 2, head and rostrum (lateral); 3, maxilla (dorsal); 4, aedeagus (dorsal); 5, aedeagus (lateral); 6, female sternum 8 (ventral); 7 , hemisternite (ventral); 8 , spermatheca (lateral).

Description. Habitus (Fig. 1). Small (total length 3.0-3.9 mm). Integument dark brown. Vestiture of pronotum and elytra of subcircular, very small scales, lacking setae.

Frons with fovea. Eyes ovate, large, flat. Rostrum as long as pronotum, lacking dorsal carinae. Scrobes (Fig. 2) deep, reaching eyes, ventral carina lacking teeth. Pterygia not developed. Epistome flat, reduced. Mandibles small, external face with two setae. Maxillae (Fig. 3) with mala lacking teeth. Antennae (Fig. 3) inserted in the middle of the rostrum; scape not reaching hind margin of eye when resting in scrobe; funicular article 1 longer than 2, articles 3-6 subglobose; club ovate.

Pronotum (Fig. 1) subcircular, with expanded sides; postocular lobes absent. Metepisternal suture present. Scutellum very reduced.

Elytra (Fig. 1) elongate, as wide as pronotum, convex; humeri rounded, not prominent; tubercles absent.

Legs with femora robust, clavate; tibiae mucronate, lacking spurs; tarsomeres 3 bilobate.

Male. Aedeagus (Figs. 4, 5) symmetrical, robust in lateral view, sides subparallel.
Female. Sternum 8 (Fig. 6) with reduced plate, lacking sclerotized arms, apical margin with short, strong setae; apodeme strong, straight. Hemisternites (Fig. 7) short, styli apical, reduced, with few short setae. Spermatheca (Fig. 8) with nodulus and ramus not developed.

Cladistic placement. Originally described as Erirhininae, Haversiella was subse-
quently placed by Kuschel (1971) in the Tychiinae, but later transferred (without comment) by him to the Listroderini (Kuschel, 1986); the latter is now a synonym of Rhytirrhinini (Kuschel, 1990). Among Rhytirrhinini, two synapomorphies unite Haversiella to Palaechtus Waterhouse and related genera from Tristan da CunhaGough, and the American genera Listronotus Jekel, Lixellus LeConte, and Neopachytychius Hustache: the long, slender, curved rostrum, and the undeveloped pterygia. Among these genera Haversiella is most closely related to Neopachytychius, based on the character states of antennae inserted in the middle of the rostrum and the convex pronotum. In addition to the autapomorphic maxillary mala lacking teeth, Haversiella presents a mosaic of characters that also occur in other Rhytirrhinini, such as subcircular pronotum and absence of postocular lobes (e.g., Falklandius Enderlein and Antarctobius Fairmaire), absence of spurs (e.g., Philippius Germain), and reduced sternum 8 plate (e.g., Falklandius).

Distribution and habitat. Haversiella albolimbata is distributed in southern South America, on the Falkland Islands and the Magellanic moorland of southern Chile and Argentina. This distribution corresponds to the Subantarctic dominion (Cabrera and Willink, 1973). A generalized track connecting these areas is shared with other genera of the tribe (Morrone, 1992).

## Haversiella albolimbata (Champion)

Haversia albolimbata Champion, 1918:186; Klima, 1934:144 (cat.); Blackwelder, 1947:826 (list); Ringuelet, 1955:434 (biog.).
Haversiella albolimbata; Schweiger, 1958:42 (biog.); Robinson, 1984:8 (list); Wibmer and O'Brien, 1986:120 (checklist).

Redescription. Male (Fig. 1). Scales iridescent green; white scales forming a stripe at the sides of pronotum and elytra, and median white longitudinal line on pronotum.

Rostrum (Fig. 2) 4.0-5.5 $\times$ longer than wide, 1.2-1.3× longer than pronotum. Antennae (Fig. 2) with article 1 of funicle $1.6-1.9 \times$ longer than 2 .

Pronotum (Fig. 1) 0.8-0.9 $\times$ longer than wide.
Elytra (Fig. 1) 2.0-2.5× longer than wide; even striae conspicuous, intervals flat. Aedeagus (Figs. 4, 5) with rounded apex, apodemes shorter than aedeagal body.
Female. Sternum 8 (Fig. 6). Hemisternites (Fig. 7). Spermatheca (Fig. 8).
Total length 3.0-3.9 mm.
Type material. The lectotype male (here designated) bears the following labels (each separated by square brackets, with a slash to separate each line): [ $\hat{\text { ] }}$ [Falkland Is./ 73-22] [Ann. \& Mag. 1918./ Haversia/ albolimbata, Ch.] [Haversia/ albolimbata/ GC] [SYN-/ TYPE] [Haversia albolimbata Ch./ lectotype ${ }^{\text {o/ }}$ / Morrone des. 1994] (BMNH). One paralectotype with the same data (BMNH).

Other material examined. ARGENTINA. Falkland Islands: E Falkland, Mt. Usborne, 700 m , "dry grassland with mosses," 3-II-1985, Lewis (3 BMNH). Tierra del Fuego: Bahía Buen Suceso, 23/26-IV-1971, Flint \& Hevel (4 USNM). CHILE. Magallanes: Isla Vidal Gormaz, 31-I/6-II-1976, Benegas (1 MHNS).

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# FOSSIL CYDNIDAE (HETEROPTERA) IN THE DOMINICAN AMBER 

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#### Abstract

Three new fossil species of burrower bug (Heteroptera: Cydnidae) are described based on four specimens from Tertiary Dominican amber. The three new species, Dallasiellus succineus, Amnestus electricus, and Amnestus priscus, are assigned to extant genera.


Burrower bugs (Cydnidae: Heteroptera) are common insects in tropical habitats. They are also among the commonest representatives of the fossil Heteroptera in Tertiary shale deposits (Scudder, 1890; Schaefer and Crepet, 1986). They are much less common as amber fossils, and in fact, have yet to be found in the extensive deposits of amber from the Baltic Tertiary. There is one report of a thaumastellid, a cydnid in the broadest sense, from Cretaceous Lebanese amber (Dolling, 1981) and two specimens are known from Oligo-Miocene amber from Chiapas, Mexico (Thomas, 1988). This is the first report of the family in the Dominican amber.

The age of the Dominican amber is problematic. Using nuclear magnetic resonance spectroscopy, Lambert et al. (1985) calculated a range of ages from 15 to 40 million years, depending on the deposit from which it originated. Grimaldi (1987, 1991) though, recommended caution before accepting any of the NMR dates. There are some 10 major amber mines in the Dominican Republic but only one, the Palo Alto mine near Santiago in the Cordillera Septentrionale has been directly dated by stratigraphy. The Palo Alto amber deposits intercalate with Lower Miocene marine strata bearing foraminifera that correlate to 20-23 MYBP (Baroni-Urbani and Saunders, 1982). Because the amber is secondarily deposited in estuarine sediments giving rise to these strata, the estimated age of the amber is a minimum one, though presumably not much older. The rock surrounding these deposits has been dated at 25-40 MYBP (Poinar, 1992).

Unfortunately, many amber specimens are purchased under conditions that obscure their origin. Of the four cydnid fossils available for study, three have labels only indicating that they were purchased in the Dominican Republic. Grimaldi (1987) indicated that an age of Lower Miocene is applicable to the bulk of Dominican amber. The fourth specimen bears the indication "La Toca." According to Poinar (1992) the La Toca mine is the oldest deposit on the island and based on NMR spectroscopy has an estimated age of 40 MYBP (Eocene). An Eocene age for this specimen can be accepted only with great reservation. It clearly belongs to the extant genus Amnestus which is neotropical in distribution, ranging from the southern United States to Brazil. Until the age of these deposits can be confirmed the less precise designation of Tertiary is preferred.

## MATERIALS AND METHODS

These amber specimens were prepared (cut, ground and polished) using the methods of Grimaldi (1993). The inclusions were studied under an ordinary dissecting microscope, with the amber immersed in mineral oil.

## RESULTS AND DISCUSSION

The four specimens were found to represent three new species in two genera. The genera to which they are unquestionably assignable are modern forms extant in the Caribbean region. The species, though differing from extant forms, are clearly related to the Caribbean fauna.

## Dallasiellus (Dallasiellus) succineus, new species

(Fig. 1)
Description. Elongate, oval; depressed above, convex below; length 7.0 mm ; color black with hemelytral membrane clear. Margin of juga carinate, apices convergent but not contiguous, each jugum with three submarginal setigerous punctures; canthus of eye with stout laterally directed seta. Dorsum of head impunctate, smooth, flat, without impression at apex of clypeus. Antennal segments II and III subequal, slightly longer than I, slightly shorter than IV or V which are subequal in length. Rostrum extends slightly past mesocoxae in type, perhaps reaching metacoxae when completely reposed.

Pronotum slightly wider than long; lateral margins with five submarginal setigerous punctures. Each costa with one setigerous puncture. Post-frenal portion of scutellum brief, narrow, apex obtuse; clavus almost reaches apex. Posterior disc of scutellum with coarse scattered punctures. Mesocorium with one row of punctures closely adpressed to claval suture.

Evaporatorium without interruption on mesopleura; of metapleura also entire, its margin straight, not deeply concave, extending to lateral edge of metapleura anteriorly. Orificial peritreme obscured in type. Protibia compressed, clavate; ental margin with three long socketed spines, ectal margin with seven socketed spines successively longer distally. Meso- and metatibia terete with numerous uniform spines on all surfaces; metatibia lacking subbasal angulation.
Holotype. Female, labeled: AMNH DR-10-13, Amber: Dominican Republic.
Remarks. In both Froeschner's (1960) original key to the species of the subgenus Dallasiellus, and in his later (1980) modified key, the fossil specimen falls out with the Central American species D. bacchinus Froeschner. It differs from that species in lacking the characteristic impression of the clypeus and in having only one row of punctures on the mesocorium. The only recent species in the nominate subgenus of Dallasiellus occurring in the Antilles is D. lugubris Stål (Froeschner, 1960) and I consider the fossil example to be closest to that species. Dallasiellus lugubris is widespread, occurring from the United States to Argentina, including the West Indies. Froeschner (1960) notes that it is a polytypic form encompassing several nominal segregates, all of which he treats as synonyms. Material used for comparison was from Belize and Mexico. The salient differences are the larger size of the amber form and the presence of only one row of punctures on the mesocorium (versus two in $D$. lugubris).


Fig. 1. Dallasiellus succineus, new species.

## Amnestus electricus, new species

(Fig. 2)
Description. Form oblong, subparallel; dorso-ventrally compressed. Length, 2.0 mm . Color tan with hemelytral membrane clear.

Clypeus distinctly longer than juga by about two-thirds its width; apex with four pegs. Each jugum with four marginal pegs, posterior pair smaller than anterior pair, submargin with five setigerous punctures. Antennae appearing four-segmented as segment II is minute.

Pronotum with coarse scattered punctures except on calli; submargin with eight setigerous punctures; length slightly less than hemelytral corium. Scutellum slightly longer than wide; lateral margins closely punctate. Claval commissure present; clavus with triple row of punctures; mesocorium with two long and one short row of punctures; exocorium with short oblique rows of punctures.

All femora unarmed. Protibiae strongly expanded apically with four large curved


Fig. 2. Amnestus electricus, new species.


Fig. 3. Amnestus priscus, new species.
spines at apex and four socketed spurs on ectal margin, successively larger towards apex. Mesotibia with eleven slender spines on ectal margin.
Holotype. Female, labeled: "AMNH DR-10-22, Dominican Republic, La Toca." Deposited AMNH. Paratype: Female, labeled: "AMNH DR-8-389, purchased in Santo Domingo." Deposited AMNH.
Remarks. The closest extant species is Amnestus pusio (Stål), which occurs from the United States to Brazil, including the Greater Antilles. The fossil species differs in having the pronotal calli impunctate, a longer scutellum and a more densely punctate corium.

Amnestus priscus, new species
(Fig. 3)
Description. Form elongate-oval, dorso-ventrally compressed; color tan except hemelytral membrane transparent. Length 2.6 mm .

Clypeus only slightly longer than juga; apex with four pegs. Margin of each jugum with five pegs and four long submarginal setae. Antenna appearing four-segmented as segment II is minute.

Pronotum slightly wider than long with a transverse furrow, coarsely and densely punctate posterior to furrow, sparsely punctate anterior to furrow. Anterolateral pronotal margin carinate, arcuate in dorsal view with five setigerous punctures. Scu-
tellum slightly wider than long with regularly scattered large punctures. Claval commissure present. Clavus with three rows of small punctures; mesocorium with coarse shallow punctures except at middle of disk; exocorium with scattered shallow punctures. Posterior margin of corium strongly sinuate.

Profemora with strong bifid spine at middle of ental margin directed obliquely away from base. Metafemora with subapical oblique spur about two-thirds width of femur. Protibia flattened, without angulate projection, expanded apically with four stout spines on ectal margin and apex, one other at apex of ental margin. Meso- and metatibiae subterete with numerous slender spines on all surfaces.
Holotype. Male, labeled: "Amber: Oligomiocene Dominican Republic, specific locality unknown. Purchased from Ramon Martinez, Santiago. AMNH No. DR-848."

Remarks. This specimen agrees in most characters with the recent Cuban species, Amnestus trimaculatus Froeschner. It differs by lacking an angular projection on the protibia. Also, it differs in the distribution of punctures on the exocorium which is a definitive feature of $A$. trimaculatus (Froeschner and Baranowski, 1970). The markings on the hemelytra found in A. trimaculatus are not in evidence, but this is perhaps artifactual.

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# A NEW CASE OF PARTHENOGENESIS IN BEETLES: LONGITARSUS MELANURUS (MELSHEIMER) (COLEOPTERA: CHRYSOMELIDAE) 

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Abstract. - Parthenogenesis as previously known in five genera of Chrysomelidae (Leaf Beetles) is reviewed. Evidence is presented for a new case of parthenogenesis in Chrysomelidae, Longitarsus melanurus (Melsheimer), recorded feeding on an introduced plant, Echium vulgare Linnaeus (Boraginaceae), in Massachusetts, New York, Pennsylvania, and Virginia.

Parthenogenetic reproduction (egg development without fertilization) is a kind of genetic polymorphism which occurs sporadically in insects with relatively few cases in beetles. In Coleoptera, especially Polyphaga, the most common parthenogenesis is developmentally apomictic or ameiotic, producing all females, usually referred to as thelytoky. These parthenogenetic species often have geographical differences, thus some populations may be parthenogenetic while populations of the same species from a different geographic area may be bisexual. There are some advantages of thelytoky in that females can spend all of their time feeding and reproducing rather than searching for mates, thus, the reproductive potential of the population is higher. A disadvantage of thelytoky is that the long-term effect may be loss of the ability to adapt to changing environments (Chapman, 1971). Considering the large number of species of Coleoptera, parthenogenesis has been discovered in relatively few families or species, but certainly many await discovery (Smith and Virkki, 1978). Probably the best studied case of thelytoky in Coleoptera is that of the polyploid weevils such as Otiorhynchus (Curculionidae) in which many species demonstrate this phenomenon (see Suomalainen and Saura, 1973; Saura et al., 1976; Smith and Virkki, 1978).

In the Chrysomelidae, however, there are only ten reported cases, including six in one genus, of parthenogenesis and two of these are Alticinae. Petitpierre (in litt.) also mentioned possible instances of polyploidy (as yet unproven) in Aulacophora femoralis (Motschulsky) (Galerucinae) and Dicladispa armigera (Olivier) (Hispinae). The first reported case of parthenogenesis in Chrysomelidae, possibly the first of any beetle, was in Gastrophysa raphini Herbst (=viridula DeGeer) (Chrysomelinae) by Osborne (1879, 1880a, b). However, apparently little further cytogenetic research has been conducted on G. viridula (see Petitpierre et al., 1988). Another chrysomeline genus, Calligrapha, has 36 known species recorded in North America and another 37 recorded from Central and South America (Wilcox, 1975). After examining 17 Calligrapha species cytologically, Robertson (1964a) first reported that six of these species were parthenogenetic (vicina Schaeffer, virginea Brown, alnicola Brown, apicalis Notman, ostryae Brown, and scalaris (LeConte)). C. scalaris had parthenogenetic or bisexual populations depending on the location (Robertson, 1964a), but the parthenogenetics were all tetraploid. Robertson (1966) studied Calligrapha further and in greater detail, including the foodplants, distribution, sex ratios, egg production,
and chromosome configuration of both bisexual and parthenogenetic species. He also discovered supernumerary chromosomes in C. philadelphica L. (Robertson, 1964b).

Smith (1971) referred to the situation in Calligrapha as studied by Robertson (1964a, 1966) as "pseudoparthenogenesis" apparently because he interpreted Robertson's data as indicating a type of facultative (i.e., that some populations or some generations produced only females and others were bisexual) rather than the usual obligatory parthenogenesis. It seems that further genetic study of Calligrapha species and their populations is warranted.

The best known case of chrysomelid parthenogenesis is Bromius (formerly Adoxus) obscurus (L.) (Eumolpinae). This case represents a geographical parthenogenesis where the North American populations of B. obscurus are diploid (bisexual) and the European populations are apomictic triploids (females only) (Smith, 1971). Although parthenogenetic B. obscurus was first reported long ago (Jobert, 1881; Jolicoer and Topsent, 1892), it has been studied quite thoroughly by Suomalainen (1965) and Lokki et al. (1976). Jobert (1881) examined over 3700 specimens without finding any males. In the early 1900s there were a few reports of rare B. obscurus males in Europe; however, Lokki et al. (1976) cytologically confirmed parthenogenesis in this species, but stated that even obligatory parthenogenetic species may occasionally produce a few males.

In North America B. obscurus feeds on grapes (Vitis), whereas the populations in Europe feed on Chamaenerion or Epilobium (Onagraceae) (Suomalainen et al., 1987; Mohr, 1966). Lokki et al. (1976) pointed out that in all parthenogenetic animals the bisexual race is assumed to be the ancestral one from which the parthenogenetic one evolved, thus the North American populations are ancestral for B. obscurus. Lokki et al. (1976) also stated that, compared to other parthenogenetic insects they had studied (e.g., the flightless moth, Solenobia triquetrella (Hübner) and the flightless weevil, Otiorhynchus scaber (L.)), B. obscurus was genetically very monomorphic, i.e., less polymorphic. They explained this as caused by the active dispersal capability of B. obscurus. Study of genetic polymorphism in parthenogenetic insects with differing dispersal capabilities should shed light on the relationship between mutation and selection (Lokki et al., 1976).

Only two species of Alticinae have been reported as parthenogenetic. The first was Altica lazulina LeConte which is distributed in Washington, Oregon and Idaho (Hatch, 1971), and reported from Montana and Colorado (Wilcox, 1975) as well as from British Columbia (Smith and Virkki, 1978). This Altica was reported by Smith (1960, 1971), Smith and Virkki (1978) and Suomalainen et al. (1987) as producing triploid thelytokous parthenogenesis (in the laboratory only). This species is apparently bisexual in nature, Hatch (1971) gives aedeagus characters in his key and male specimens are present in the LeConte and Horn collections in the Museum of Comparative Zoology at Harvard University (MCZ). Robertson (1966) said that Smith (unpubl.) found $A$. tombacina (Mannerheim) to be a triploid parthenogenetic; however, probably this was the preliminary determination for A. lazulina. Smith (1960) listed chromosome information for 8 species of Altica, all normal diploid bisexuals, but there was no mention of $A$. tombacina or lazulina. However, this genus is extremely difficult taxonomically and it has never been revised in this century; therefore, the identity of specimens are usually suspect.

The second Alticinae reported as parthenogenetic was Chaetocnema perplexa Blake
(Virkki et al., 1989). Even though Blake (1941) described C. perplexa as bisexual, she stated that "although there were many specimens, there were very few males in any collection." S. Clark (in Virkki et al., 1989 and pers. comm.) says that all specimens he has examined from the West Indies have been females. Virkki et al. (1989) sampled hundreds of C. perplexa from sweet potatoes (Ipomoea spp.) in Puerto Rico and all were females; they reasoned that absence of males was an indication of parthenogenesis. Many of these C. perplexa were infested by a nematode (Howardula sp.) and Virkki et al. (1989) found that this infestation suppressed oogenesis in over one half of the beetle populations. They speculated that this pressure, possibly in combination with other unexplained factors, may be enough to produce the observed parthenogenetic populations.

The present study concerns parthenogenesis in a third Alticinae, Longitarsus. Longitarsus is the most biodiverse genus in the Chrysomelidae with between 600-700 described species worldwide; it is also the most difficult taxonomically and, like most insect groups, relatively little is known about the biology of most species. Furth (1980b) reported that, more than any other chrysomelid group, Longitarsus had a significant percentage of species with intra-specific wing length polymorphism (flightlessness). Even though many species of Longitarsus have been examined cytogenetically (Petitpierre et al., 1988; Segarra and Petitpierre, 1988), as yet none have been found with any unusual characteristics.

## METHODS AND RESULTS

In 1983 E. R. Hoebeke (Cornell University) sent the author 9 female specimens of a Longitarsus species for determination that he had collected in New York (Onondaga Co., Solvay railroad yards, 14 May 1983) feeding on Echium vulgare L., a Boraginaceae introduced to North America a very long time ago (see Discussion). After comparison with specimens in the author's extensive Palearctic Longitarsus collection and with the literature, and dissection and study of the female spermatheca, the author determined that this Longitarsus species was not a Palearctic species but rather a Nearctic species. At that time the author did not attempt to determine the exact species name.

On 7 July 1991 the author collected 55 specimens of the same Longitarsus feeding on E. vulgare along Memorial Drive in Cambridge, Massachusetts (Middlesex Co.) near the city border with Watertown. Like many borage-feeding Longitarsus which the author has collected in the Palearctic, this species was feeding on both surfaces of $E$. vulgare leaves, especially on the rosette leaves. These specimens were kept alive on their foodplant under ambient conditions at the MCZ and were observed to be actively feeding and laying eggs. After one week the specimens were killed with ethyl acetate and examined, including spermatheca, and found to be all females. With the aid of the MCZ's historical collections of J. L. LeConte, G. Horn, F. V. Melsheimer, H. C. Fall, etc., this species was determined to be L. melanurus (Melsheimer). Based on the author's extensive field experience in the Palearctic with many borage-feeding Longitarsus (Furth, 1980a), if females are abundantly ovipositing, males should be present. The author returned to the same site 10 days later ( 17 July) and collected 41 more specimens-all proved to be females of L. melanurus; therefore, all 96 specimens from this site were females. An attempt was made to collect more spec-


## 0.5 mm

Fig. 1. Spermatheca of Longitarsus melanurus (Melsheimer), lateral view.
imens from the same site in Cambridge on 7 July 1993; however, the E. vulgare plants had been cut down apparently several weeks previously and only a few rosettes remained. As a result only 5 specimens were collected in 1993, all females; therefore, the population of $L$. melanurus still exists at the Cambridge site.
L. melanurus spermathecae from the Massachusetts and New York populations were examined. The spermatheca (Fig. 1) is typical for Longitarsus; however, preliminary study indicates more than the normal amount of morphological variability in the coiling pattern of the spermathecal duct. In this genus the coiling pattern of the duct is normally quite constant with little variability; however, there are some exceptions (Leonardi, 1973).

Longitarsus melanurus (Melsheimer) was originally described from Pennsylvania, but more recently recorded from the eastern USA and Canada (Wilcox, 1975). Blatchley (1910) figured L. melanurus and recorded it as frequent in southern and rare in northern Indiana, taken from roadside vegetation. With the aid of E. R. Hoebeke, the author was able to examine and determine the following series of $L$. melanurus collected recently from E. vulgare and deposited in the insect collection at Cornell University: Pennsylvania, Schuykill Co., Port Carbon, 18 July 1985, A. G. Wheeler, Jr. (13 specimens); Virginia, Rockbridge Co., I-81 S. Natural Bridge exit, 2 July 1987, A. G. Wheeler (106 specimens); Pennsylvania, Dauphin Co., Harrisburg, 6 July 1987, E. R. Hoebeke ( 27 specimens). All of these specimens are females; most are deposited at Cornell University with samples of each in the author's collection. The author has also carefully examined and redetermined all of the specimens of $L$. melanurus in the collections of the MCZ (LeConte, Horn, Melsheimer-Zeigler, Fall, and general). In the MCZ collections there were true L. melanurus from: Quebec, Maine; New Hampshire; New York; Pennsylvania; West Virginia; North Carolina; Michigan; Illinois; "Dakota"; Kansas; Missouri; Texas; Iowa; and Colorado-all of these specimens are also females. No apparent type specimen or type series was found in any of the MCZ collections, including the Melsheimer material. With the assistance of
A. Provansha, the author was able to examine the collection at Purdue University, including the W.S. Blatchley collection, which contains 10 specimens of $L$. melanurus from 8 counties of Indiana-all are females. Thanks to the late Edward Balsbaugh, Jr., the author examined a small series of $L$. melanurus from the North Dakota State University insect collection which contains 11 specimens from North Dakota, Minnesota and Pennsylvania-all females.

## DISCUSSION

This study provides quite convincing evidence of the parthenogenesis in Longitarsus melanurus, the sixth genus and eleventh species of Chrysomelidae reported with this phenomenon. As with the case of parthenogenesis in Chaetocnema perplexa reported by Virkki et al. (1989) from Puerto Rico, the evidence for parthenogenesis in L. melanurus is circumstantial and statistical (i.e., absence of males) rather than cytogenetic. Because Longitarsus have root feeding larvae, fairly elaborate controlled facilities would be required to rear them in order to verify that all progeny are female. Also cytogenetic techniques necessary to prove parthenogenesis are rather complicated (Virkki, in litt., Petitpierre, in litt.) and are beyond the scope of the present study.

The all-female samples from E. vulgare at the Cambridge, Massachusetts site together with the same from New York, Pennsylvania, Virginia in the collections of Cornell University and of the author, as well as the few smaller museum samples listed above, indicate quite strongly that most and probably all populations of $L$. melanurus are parthenogenetic, probably thelytokous polyploidy as known in other chrysomelids such as Calligrapha and Bromius. Of course, it remains to be proven whether the parthenogenesis in $L$. melanurus has a geographical bisexual component as do the European and North American populations of Bromius obscurus.

Because Echium vulgare (Viper's Bugloss) is an introduced plant in North America, it is interesting to speculate as to the true foodplant for L. melanurus. Leighton (1986) indicates that $E$. vulgare was present in New England early in the seventeenth century; therefore, it was introduced more than 350 years ago and L. melanurus could have been using E. vulgare as a foodplant since then. Also Gray (1848) lists E. vulgare as "rare in the Northern States, a troublesome weed in Virginia." There are relatively few native Boraginaceae in eastern North America, especially any that may be related, including chemically, to Echium, the most likely may be native species of Lithospermum or Onosmodium which are in the same tribe as Echium (Riedl, 1968; Fein-brun-Dothan, 1978). Another possibility may be native species of Cynoglossum, in a closely related tribe. All three of these other genera share some chemical substances with Echium, for example, bornesit, fructane and allantoin, but the known chemistry of Echium seems much less diverse than that of Lithospermum (Hegnauer, 1964, 1989).

Virkki et al. (1989) speculate that heavy infestation by a nematode may have caused parthenogenesis in Chaetocnema perplexa. If $L$. melanurus is actually bisexual in some populations, then switching to a non-native foodplant may be a synergistic contributing factor to parthenogenesis in this species. However, the evidence suggests that all populations of $L$. melanurus are parthenogenetic and, therefore, this type of genetic polymorphism apparently also is reflected in its ability to switch to a non-
native foodplant. The Massachusetts population of L. melanurus is macropterous and fully able to fly and to disperse to other stands of E. vulgare or to its native foodplant. Part of the theory of thelytokous parthenogenesis is that an all-female population can concentrate its energy on reproduction, i.e., increased fecundity. A similar principle pertains to the theory of intra-specific wing polymorphism present in many species of Longitarsus, in which wing reduction allows increased fecundity (Furth, 1980b).

Chapman's (1971) definition of thelytokous parthenogenesis states that the disadvantageous long-term effect is loss of ability to adapt to changing environments; however, the present study demonstrates that $L$. melanurus has been able to establish at least several widely disjunct populations feeding on a non-native foodplant. If $L$. melanurus is indeed a totally parthenogenetic species, then, contrary to the principle mentioned above, it does seem to be able to adapt to changing environments such as a new foodplant in disjunct regions. Although it may seem that the switch of $L$. melanurus to the introduced $E$. vulgare may be recent in evolutionary time, other genetic phenomena such as wing polymorphism apparently occur rather rapidly in this beetle genus and others (Furth, 1980b).

The purpose of this study is primarily to report the existence of parthenogenesis in Longitarsus melanurus and to encourage further research concerning its genetics as well as its foodplant switching. The existence of these phenomena in L. melanurus should provide a variety of interesting topics for future investigation.

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## APPENDIX

After this manuscript was submitted, the author was contacted by Mr. Andrew H. Williams (Department of Entomology, University of Wisconsin, Madison) concerning his survey of Onosmodium molle Michx. (Boraginaceae), a plant listed by the Wisconsin Bureau of Endangered Resources as a species of Special Concern. Mr. Williams found adults of $L$. melanurus (determined by E. Riley; Texas A\&M University, College Station, and later confirmed by the author) feeding on leaves of $O$. molle at several localities in Wisconsin (Dane, Grant and Iowa counties) on dates ranging from May 13 to July 22. In addition, he found one adult feeding on a leaf of Cynoglossum officinale L. (a Boraginaceae introduced from Europe). This discovery of $L$. melanurus feeding on a native Onosmodium confirms the author's prediction made in the Discussion of this paper.

# A REVISION OF THE GENUS THASUS (HEMIPTERA: COREIDAE: COREINAE: NEMATOPODINI) 

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#### Abstract

The neotropical coreid genus Thasus is revised. Of the eight species, five (carchinus, luteolus, neocalifornicus, odonnellae, and rutilus) are described as new. One of these, T. neocalifornicus, extends into the southwestern United States, where it has been misidentified as $T$. gigas or acutangulus. The species are keyed and analyzed cladistically, their distributions are discussed, and aspects of their morphology are illustrated.


In 1865, Stål removed from Pachylis LePeletier \& Serville 1825 three species, heteropus (Latreille), gigas (Klug), and acutangulus (Stål), to a new genus, Thasus. Although he did not distinguish between the two genera in 1865, he had in effect done so earlier: in 1862, Stål separated the three species now in Thasus from those now in Pachylis, by the dilation of the hind tibia; this, in Thasus, occurs on both sides of the tibia and, in Pachylis, occurs only ventrally. In 1867, he used these characters in a key to separate these genera.

Since Stål's work, no systematic study has been made on Thasus, which is surprising for two reasons. First, the largest members of the genus are possibly the largest of the terrestrial Heteroptera and, in the suborder, are perhaps surpassed in size only by members of the Belostomatidae. Second, the species of the genus which extends into southwestern United States has never been satisfactorily identified (see below, and discussion in Froeschner, 1988): sometimes identified as T. gigas, and sometimes as $T$. acutangulus, the United States species is actually a new one, $T$. neocalifornicus sp.n. No other species of Thasus is known to occur in the U.S.

Here we redescribe the three species, describe five new ones, key all eight, and discuss briefly their cladistic relationships.

The following abbreviations are used in the text (see Heppner and Lamas, 1982): American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Ernst Heiss Collection (CEH); Carnegie Museum of Natural History, Pittsburgh (CMP); Cornell University Insect Collection (CU); Field Museum of Natural History, Chicago (FMNH); Florida State Collection of Arthropods, Gainesville (FSCA); Instituto de Biología de la Universidad Nacional Autónoma de México (IBUNAM); Los Angeles County Museum (LACM); Texas A\&M University, College Station (TAMU); University of California, Berkeley (UCB); Universidad Central de Vene-

[^4]zuela, Escuela de Agronomia, Maracay (UCV); Universidad Central de Costa Rica, Museo de Entomología (UCCR); University of California, Riverside (UCR); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM).

Thasus Stål 1865:174
Pachylis acutangulus Stål 1859:439; designated by O'Shea (1980)
Redescription (modified from O’Shea [1980]): Body very large ( $\delta: 29-43$, : $: 28-40$ mm long), broad, stout, somewhat depressed (Figs. 1-8). Head subquadrate; postocular tubercles forming smooth curve with eye; antennifers wide, close together; tylus projecting slightly anterior to antennifers. Antennae (Figs. 9-16) long, slender; segments 1 , 2 , 4 terete, 3 dilated, dilation symmetrical or asymmetrical; 1 relatively stout (especially apically), at least slightly clavate; 4 fusiform, slightly curved; antennal formula: $4>1>2=3$, except $T$. gigas $(1=4>2=3)$ and $T$. neocalifornicus ( 1 $>2=3=4$ ). Pronotum steeply declivent; callar region and collar clearly demarcated; lateral margins slightly nodulous or crenulate, anterior angles obtuse or rounded, humeral angles subobtuse to slightly produced into a spine; posthumeral, posterior margins smoothly sinuate; posterior angles rounded. Scutellum with broad transverse ridge anteriorly, posterior one-third slightly raised. Mesosternum without median longitudinal groove. Thoracic pleura with or without large pale hirsute areas. Metathoracic scent gland opening placed relatively laterally. Rostrum extending to or just beyond midmesosternum. Posterior trochanters of male armed with spine; all femora armed at least distally on ventral surface with spines; posterior femora incrassate, much more so in males (Figs. 17-19), dorsal surface smooth, ventral surface with spines; posterior tibiae of both sexes dilated equally ventrally and dorsally, male's ventral dilation with stout spine about two-thirds from base. Abdominal segments with spines (often large) at posterior corners. Spiracles in anterior third of sterna, closer to anterior than to lateral margins of abdominal segments. Male's genital capsule with sublateral projections on posterior margin; paramere relatively small and slender, with curved tip of "swan's neck" type (Figs. 20-22). Female's second valvula with heavily sclerotized tooth, this broad, flattened, bent inward, long or moderately long, tip variable; female connexivum 7 with spine (except T. luteolus and acutangulus); spermatheca (Figs. 23-29) oval, end away from duct tapered; spermathecal duct coiled distally and proximally, swollen proximal to distal coiling. Diagnosis: Thasus is a group of very large, stout, brown species, with dilated hind tibiae and dilated third antennal segments. The genus most likely to be confused with Thasus, is Pachylis, which is also large, stout, brown, and has the dilations.

In Thasus the metatibia is equally dilated on both sides of the midline (which can be recognized by a ridge [Figs. 17-19], which is the tibia itself). When viewed from the side, each border of the tibial ridge is equal. In Pachylis females, the metatibial dilation occurs only on one side of the ridge and, when viewed from the side, each border is highly asymmetrical; in males, the dilation occurs on both sides, but is also highly asymmetrical.

The dilation of the third antennal segment is unequal (asymmetrical) in Pachylis, and in four of the eight species of Thasus (T. rutilus, heteropus, luteolus, and odonnellae); in the last three of these species, and in Pachylis, the dilation itself is relatively small.


Figs. 1-8. Dorsal views of Thasus spp. 1. Thasus acutangulus (Stål). 2. T. carchinus sp.n. 3. T. gigas (Klug). 4. T. heteropus (Latreille). 5. T. luteolus sp.n. 6. T. neocalifornicus sp.n. 7. T. odonnellae sp.n. (type). 8. T. rutilus sp.n.



Figs. 9-16. Antennae of Thasus spp. (pale areas red-orange, stippled areas brown). 9. T. gigas (Klug). 10. T. carchinus sp.n. 11. T. rutilus sp.n. 12. T. acutangulus (Stål). 13. T. neocalifornicus sp.n. 14. T. heteropus (Latreille). 15. T. luteolus sp.n. 16. T. odonnellae sp.n. (type).

The genera Melucha Amyot et Serville, 1843 and Meluchamixia Brailovsky, 1987 might also be confused with Thasus. Both are smaller than Thasus, however (Melucha less than 25 mm long, Meluchamixia about 25 mm long). The metatibia of Melucha is dilated, but the third antennal is not (O'Shea, 1980); also, the distance between the coxae in Thasus is nearly equal to the coxa-lateral margin distance, whereas in Melucha the intercoxal distance is much less (Stål, 1867). The metatibia of Meluchamixia is only slightly dilated, and the third antennal is asymmetrically dilated (Brailovsky, 1987).

Finally, Vivianadema Brailovsky, 1987, 31 mm long, is as large as some Thasus or Pachylis. However, the humeral angles of Vivianadema are very broadly produced, almost winglike (fig. 2, in Brailovsky, 1987).


Figs. 17-19. Hind legs of Thasus spp. 17. T. odonnellae, male (type) 18. T. gigas, male. 19. T. gigas, female.

O'Shea (1980) gives a key to the nematopodine genera, although it does not include Vivianadema and Meluchamixia, both described in 1987. Brailovsky's key (1987) includes only species similar to Thasus; unfortunately, it omits Pachylis.
Discussion: Pachylis and Thasus have similar postocular tubercles (O'Shea, 1980), apparently an autapomorphy. We therefore believe these two to be sister groups.


Figs. 20-22. Parameres of Thasus spp. 20. T. gigas (type) (two views). 21. T. heteropus. 22. T. odonnellae (type).


Figs. 23-31. Spermathecae of Thasus spp. and Pachylis spp. 23. T. acutangulus (type). 24. T. gigas. 25. T. heteropus. 26. T. luteolus. 27. T. neocalifornicus. 28. T. odonnellae (paratype). 29. T. rutilus (paratype). 30. P. laticornis. 31. P. pharaonis.

However, too little is known about the species in Pachylis, and thus about intrageneric variation, for us to be certain. For example, as in Thasus, both unicolored Pachylis as well as Pachylis with yellow corial veins occur; but apparently only P. laticornis annulipes Blöte has banded legs (Blöte, 1938), like several Thasus species.

Further, the phylogenetic relationships of the genera likely to be close to Thasus remain unknown. A cladistic analysis is needed of the genera mentioned above.

## KEY TO THE KNOWN SPECIES OF THASUS

1. Antennal 3 entirely dark brown, dilation narrow and elliptical (Figs. 14-16) ........... 2 Antennal 3 dark brown ( $T$. carchinus) or bicolored, dilation broad (Figs. 9-13) ....... 4
2. Connexival segments $4-7$ dark brown, with yellow spots; clavus and corium with veins pale, contrasting with surface (Costa Rica) ....................... T. luteolus new species Connexival segments 4-7 dark brown, brown, or orange, without yellow spots; clavus and corium with veins unicolorous with surface 3
3. Humeral angles sharp; dilation of antennal 3 no more than $2 \times$ width of antennal 4 ; spine of fourth connexival segment barely visible; female's seventh connexival segment with or without very small spine (Colombia, Peru, Ecuador, Venezuela)
T. heteropus (Latreille)

Humeral angles obtuse; dilation of antennal 3 wider (at least $3 \times$ width of antennal 4); spine of fourth connexival segment small, visible; female's seventh connexivum with small spine (Bolivia) ............................................ T. odonnellae new species
4. Antennal 4 orange-red or brownish orange-red, subequal in length to antennal 3 (Fig.
13) (U.S.A., Mexico) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T. neocalifornicus new species

Antennal 4 dark brown or sharply bicolored, longer than antennal 3
5
5. Antennal 2 red-orange basally and dark brown distally (Fig. 12) (Mexico, Guatemala,

British Honduras, Costa Rica) ...................................... T. . acutangulus (Stål)
Antennal 2 dark brown
6
6. Antennal 4 red-orange basally and dark brown distally (Fig. 11) (Peru, Brazil, French Guiana)
T. rutilus new species

Antennal 4 dark brown
7
7. Antennal 3 unicolorous (Fig. 10) (Ecuador) ...................... T. carchinus new species Antennal 3 red-orange basally and dark brown distally (Fig. 9) (Mexico, El Salvador)
T. gigas (Klug)

Thasus acutangulus (Stål)
(Figs. 1, 12, 23)
Pachylis acutangula Stål, 1858:439
Redescription of holotype. Female: Color: Head black laterally, disk reddish-brown; ocelli ringed with black, and with yellow semicircle laterally. Antennal 1 deep reddishbrown, base and apex black; basal half of 2 and 3 orange, apical half black; 4 [missing in holotype, brown-black in other specimens]. Pronotum reddish-brown, callar region paler; collar and thin lateral line black, latter becoming yellow posteriorly; posterior edge yellow. Scutellum reddish-brown, lateral edges and apex yellow. Corium dark brown, veins yellow; membrane black. Connexival segments 3-7 dark reddish-brown posteriorly, orange anteriorly. Abdominal dorsum black. Thoracic pleura widely reddish-brown, each darkening to black near coxa and posterior edge. Anterior lobe
Table 1. Measurements (in mm) of species of Thasus (means and ranges).

|  | T. acutangulus |  |  | T. gigas |  |  | T. heteropus |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{gathered} \text { Holo- } \\ \text { type } \\ \text { \& } \end{gathered}$ | $\left(\mathrm{N}^{\circ}=3\right)$ | $(\stackrel{\&}{=} 3)$ | $\begin{gathered} \text { Holo- } \\ \text { type } \\ \delta \end{gathered}$ | $\left(\mathrm{N}^{\circ}=3\right)$ | $\left(\mathrm{N}^{\circ}=3\right)$ | $\left(\mathrm{N}^{\delta} \stackrel{\delta}{=} 3\right)$ | $\left(\mathrm{N}^{\circ}=3\right)$ |
| Total length ${ }^{1}$ | 40.0 | 37.3 (34-40) | 33.7 (32-34) | 43.0 | 40.0 (40-41) | 37.0 (36-39) | 29.0 (26-31) | 28.0 (28-29) |
| Head width across eyes | 3.2 | 3.3 (3.2-3.4) | 3.2 (3.0-3.4) | 3.6 | 3.4 (3.4-3.5) | 3.3 (3.2-3.3) | 2.7 (2.2-3.1) | 2.9 (2.7-3.0) |
| Head length from ocellar line | 2.2 | 2.4 (2.2-2.5) | 2.1 (1.8-2.3) | 2.2 | 2.6 (2.3-3.0) | 2.5 (2.3-2.7) | 2.0 (1.8-2.2) | 2.0 (1.8-2.1) |
| Interocular width | 1.8 | 1.8 (1.8) | 1.7 (1.6-1.8) | 2.0 | 2.8 (1.8-2.1) | 1.9 (1.8-2.0) | 1.6 (1.4-1.7) | 1.6 (1.5-1.8) |
| Interocellar width | 0.8 | 1.0 (0.9-1.0) | 0.9 (0.9) | 1.4 | 1.3 (1.2-1.3) | 1.3 (1.2-1.3) | 0.8 (0.8-0.9) | 0.9 (0.9-0.9) |
| Pronotal width | 14.9 | 13.0 (11.3-14.3) | 12.9 (12.5-13.4) | 13.4 | 12.8 (11.9-13.5) | $11.7(11.2-12.5)$ | 12.1 (10.8-13.1) | 12.9 (12.4-13.3) |
| Scutellar width | 4.7 | 4.9 (4.4-5.5) | 4.6 (4.4-4.7) | 4.9 | 5.1 (4.9-5.3) | 5.0 (4.6-5.1) | 3.8 (3.4-4.3) | 4.4 (4.2-4.7) |
| Scutellar length | 4.6 | 4.4 (3.5-5.3) | 3.8 (3.6-3.9) | 4.7 | 4.8 (4.4-5.2) | 4.5 (4.3-4.6) | 3.8 (3.4-4.3) | 4.2 (3.9-4.7) |
| Antennal lengths |  |  |  |  |  |  |  |  |
| I | 6.5 | 7.0 (6.8-7.5) | 6.3 (6.2-6.4) | 7.9 | 7.4 (6.9-8.1) | 6.6 (6.3-6.8) | 5.0 (4.7-5.3) | 5.0 (4.7-5.2) |
| II | 5.3 | 5.5 (5.3-5.7) | 5.4 (5.2-5.5) | 5.5 | 5.9 (5.6-6.2) | 5.2 (4.7-5.6) | 3.8 (3.6-4.4) | 3.9 (3.9) |
| III | 5.3 | 5.4 (5.2-5.5) | 5.0 (4.9-5.1) | 5.5 | 5.5 (5.2-5.9) | 5.1 (4.9-5.3) | 3.4 (3.2-3.5) | 3.1 (2.9-3.5) |
| IV | - | 8.2 (7.8-8.6) | 7.5 (7.2-7.7) | 7.5 | 6.6 (6.5-6.8) | 6.4 (6.2-6.5) | 6.8 (6.5-7.2) | 6.3 (6.0-6.5) |
| Maximal width of III | 2.5 | 2.5 (2.5) | 2.5 (2.3-2.6) | 2.6 | 2.6 (2.5-2.7) | 2.4 (2.2-2.5) | 0.6 (0.5-0.8) | 0.8 (0.8-0.8) |
| Maximal width of hind tibia | 2.7 | 2.7 (2.3-3.0) | 2.8 (2.7-2.9) | 2.5 | 2.7 (2.5-2.7) | 2.0 (1.8-2.2) | 2.0 (1.4-2.6) | 2.0 (2.0-2.1) |

[^5]Table 1. Extended.

| T. carchinus holotype 9 | T. Iuteolus |  | T. neocalifornicus |  |  | T. odonnellae |  | T. rutilus |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\underset{\delta}{\text { Holotype }}$ | $(N \stackrel{\delta}{=} 1)$ | $\underset{\delta}{\text { Holotype }}$ | $\left(\mathrm{N}_{\stackrel{\delta}{8}}^{=} 3\right)$ | $\left(\mathrm{N}^{\circ}=3\right)$ | $\underset{\delta}{\text { Holotype }}$ | ¢ | $\begin{gathered} \text { Paratype } \\ (\mathrm{N}=20 \end{gathered}$ | $\underset{\&}{\text { Paratype }}$ |
| 39.0 | 33.0 | 34.0 | 34.5 | 36.0 (35-36) | 33.0 (32-34) | 34.0 | 36.0 | 36.5 (36-37) | 35.0 |
| 3.6 | 3.2 | 3.2 | 3.4 | 3.5 (3.4-3.6) | 3.3 (3.1-3.6) | 3.4 | 3.5 | 3.5 (3.4-3.6) | 3.5 |
| 2.5 | 1.9 | 2.1 | 2.1 | 2.4 (2.3-2.5) | 2.2 (2.1-2.3) | 1.8 | 2.1 | 2.1 (2.0-2.2) | 2.1 |
| 1.9 | 1.7 | 1.6 | 1.8 | 2.1 (2.0-2.2) | 2.0 (1.8-2.1) | 1.8 | 2.1 | 2.0 (2.0) | 1.8 |
| 1.0 | 0.9 | 0.9 | 1.1 | 1.1 (1.0-1.2) | 1.0 (0.9-1.0) | 1.0 | 1.0 | 1.5 (1.0-1.1) | 0.9 |
| 14.2 | 11.7 | 12.6 | 12.8 | 13.0 (12.6-13.2) | 12.5 (11.3-13.6) | 12.7 | 13.6 | 13.4 (12.7-14.0) | 13.7 |
| 5.0 | 3.8 | 4.2 | 4.6 | 5.2 (4.6-6.3) | 4.6 (4.3-4.8) | 4.4 | 4.6 | 4.7 (4.6-4.8) | 4.7 |
| - | 4.0 | 4.2 | 4.4 | 4.4 (4.0-4.6) | 4.2 (4.1-4.4) | 4.5 | 4.8 | 4.7 (4.6-4.8) | 4.6 |
| 8.1 | 6.1 | 5.6 | 7.8 | 7.0 (6.6-7.4) | 6.1 (6.0-6.2) | 8.8 | 6.9 | $7.8(\mathrm{~N}=1)$ | 7.2 |
| 5.9 | 4.9 | 4.8 | 6.5 | 5.9 (5.8-6.0) | 5.4 (5.1-5.5) | 5.6 | 5.1 | 5.2 (5.2) | 5.2 |
| 5.2 | 4.2 | 4.3 | 5.6 | 5.5 (5.2-5.7) | 5.0 (4.8-5.1) | 4.6 | 4.6 | 5.0 (4.8-5.1) | 4.9 |
| 9.6 | 7.9 | - | 6.1 | 5.7 (5.2-6.1) | 5.0 (4.8-5.2) | 10.0 | 10.4 | 9.4 (9.4) | 8.8 |
| 2.1 | 1.2 | 1.3 | 2.0 | 2.3 (2.1-2.6) | 2.0 (1.9-2.1) | 1.3 | 1.3 | 1.8 (1.6-2.0) | 2.0 |
| 3.0 | 2.0 | 2.1 | 2.1 | 2.5 (2.5-2.6) | 2.0 (1.9-2.0) | 2.2 | 2.6 | 2.0 (1.7-2.3) | 1.6 |

of metathoracic scent gland opening black, bordered by yellow. Legs reddish-brown, apices and bases of segments black; tarsi black. Abdominal sterna reddish-brown, apicolateral borders of each black. Spiracle ringed with black. Structure: Apical $2 / 3$ of antennal 3 expanded, slightly asymmetrically. Pronotal rise about $60^{\circ}$; lateral edge crenulate; humeral angles acute. Connexivum exposed lateral to wings; connexival segments 3-7 with apicolateral spines, that on 3 very small; that on 7 smaller than that on 6. [Note: all other female specimens of T. acutangulus examined, lack a seventh-connexival spine.] Hind tibial expansion without large tooth, anterior margin smooth, posterior margin with small teeth; hind coxae with small protuberance; hind trochanter with small spine. Spermatheca: Figure 23.
Measurements: Table 1.
Holotype: In Naturhistoriska Riksmuseet (Stockholm).
Diagnosis: Recognized by its large size, humeral angles exposed, third antennal segment broad, obovate, and foliate, second antennal bicolored, fourth antennal brown to black (Fig. 12), and larger (usually above 7.30 mm ), and femora and tibiae entirely black or bright orange with anterior and posterior third black and in each case without orange rings. Features which distinguish T. acutangulus from the related T. gigas and $T$. neocalifornicus, are discussed under these species.
Biology: According to Schaefer and Mitchell (1983), the food plant record of this species (Aldrich and Blum, 1978) should refer to Pachylis laticornis (F.).
Distribution: MEXICO: Veracruz: Orizaba and Misantla. GUATEMALA: Senahu and Cerro Zunil. BRITISH HONDURAS: River Sarstoon. COSTA RICA: Guanacaste (probably misidentification) (Distant, 1881-1892; Aldrich and Blum, 1978; Walker, 1871). The records from the United States are misidentifications (see discussion of Thasus neocalifornicus).
New records: MEXICO: Veracruz: Dos Amates, Zongolica, Jalapa, Cordoba, Fortin de las Flores and Coscomatepec. Guerrero: Coyuca. Jalisco: Chamela. Oaxaca: Portillo del Rayo. Estado de Mexico: Malinalco. Morelos: Tepoztlan and Jonacatepec. San Luis Potosi: Xilitla.

## Thasus carchinus, Brailovsky \& Barrera, n. sp.

(Figs. 2, 10)
Description. Female: Color: Head, including antennals 1-4, pronotum, scutellum, and abdominal terga black with following areas yellow or orange red: space between ocellus-eye, posterolateral border including spine of humeral angle of pronotum, a very small discoidal dot on middle of posterior border of pronotum, and apex of scutellum. Clavus and corium red brown to black, with following areas pale yellow: claval and corial veins, claval commissure, posterior half of anal edge, costal margin, apical angle and apical margin of corium, and a few scattered spots between corial veins. Hemelytral membrane dark chestnut brown with blue and violet metallic iridescence and with basal angle and veins darker. Connexival segments $2-9$ with dorsal surface and spines yellow, ventral surface black; segments $2,3,8,9$ black, segments 5-7 yellow with posterior third black. Body ventrally black with following areas pale yellow or dark orange ochre: small dot in middle head region, mesopleuron, venter of trochanter, incomplete ring on apical third of femur, mesial body of tibia, pleural margin of abdominal sterna 3-7 (posterior third always black), and sternum

7 with large irregular spot on each side of midline. Structure: Dilation of third antennal segment broadly obovate and foliate; anterolateral border of prothorax nodulose; humeral angles exposed, ending in large robust spine; posterior tibiae much dilated and lanceolate, both inner and outer margins entire; posterior angle of connexival segments 4-7 each with short acute spine.
Measurements: Table 1.
Holotype. Female. ECUADOR: Province Carchi: Pallon, 1,030 m, IX-X. 1983. Deposited in CMP.
Diagnosis: This species agrees with T. acutangulus, T. gigas, and T. neocalifornicus in the shape of the third antennal segment, which is broadly obovate and foliate (Figs. 9, 10, 12). T. carchinus, new species, is recognized by the contrasting coloration of its tibiae and connexival segments, which are mostly yellow; and by the ventral body mostly black except the yellow pleural margins of abdominal sternites 3-7 (posterior third always black). The color patterns of the other species are quite distinct. Etymology: Named for the type locality, Carchi Province, Ecuador.

## Thasus gigas (Klug)

(Figs. 3, 9, 18, 19, 20, 24)
Pachylis gigas Burmeister, 1835:338
Redescription of holotype. Male: Color: Head black, with yellow-white semicircle lateral to each ocellus. Antennal segments brown-black, except 3 orange basally. Pronotum reddish-brown, except callar area black, lateral irregularly oval area pale reddish-brown. Scutellum shining mahogany, edges and apex yellow, anteromedially light reddish-brown. Corium dull mahogany, veins yellow; membrane brown-black. Connexiva brown-black, 3-7 with orange spot basolaterally. Abdominal dorsum orange, except tergum 2 and apex of 7 black. Thoracic pleura brown, yellow spot on propleuron at end of pleural suture, and yellow fascia anteriorly across meso- and metapleura. Anterior lobe of metathoracic scent gland opening black. Legs brown; all femora with two yellow rings, subbasally and subapically; coxae yellow basally. Abdominal sterna orange-red anteriorly, darkening to black posteriorly; 7 entirely black medially. Spiracle ringed with black, this black extending posteriorly from spiracle (and anteriorly on sternum 3). Structure: Apical $2 / 3$ of antennal 3 expanded, slightly asymmetrically. Pronotal rise about $50^{\circ}$; lateral edge with minute spines; humeral angles very obtuse, almost rounded. Connexivum more or less exposed lateral to wings; terga 4-7 with apicolateral spines, progressively longer. Hind tibial expansion with large sharp tooth; hind coxa with large lobelike protuberance; hind trochanter with large blunt spine. Paramere: Figure 19. Spermatheca: Figure 24.
Measurements: Table 1.
Holotype: In Museum für Naturkunde der Humboldt-Universität zu Berlin.
Diagnosis: This handsome species is similar in color and general habitus to T. acutangulus (Stål), but differs in having humeral angles rounded and obtuse, second antennal entirely brown (Fig. 9), pronotum barely declivent ( $45^{\circ}$ to $50^{\circ}$ ), posterior angle of connexival segment 7 of female with a large spine, and in both sexes femora and tibiae with orange-red rings. In T. acutangulus the humeral angles are exposed, second antennal bicolored (Fig. 12), pronotum more declivent ( $>50^{\circ}$ ), posterior angle
of connexival segment 7 of female truncated, and femora and tibiae without orange red rings. See under $T$. neocalifornicus for differences between these two species. Note: in very dark specimens, the banding of the tibiae and femora may be obscured, as may be other areas where, in paler specimens, yellow or orange occurs. Biology: In Tehuacán, in the Mexican state of Puebla, two of the present authors, together with Cristina Mayorga and Guillermina Ortega, collected this species on mesquite (Prosopis laevigata); nymphs are bright orange yellow and black and live closely aggregated; the adults are not gregarious.
Distribution: MEXICO: Nayarit: Tepic. Guerrero: Xucumanatlan and Omilteme. Veracruz: Orizaba. (Distant, 1881-1892; Walker, 1871). The records from the United States (Arizona) are misidentifications (see discussion of Thasus neocalifornicus). New records: MEXICO: Tamaulipas: km 91 carr. Tula-Ciudad Victoria. Sinaloa: Fuerte. Zacatecas: San Francisco. Durango: Nombre de Dios. Aguascalientes: Ciudad de Aguascalientes. Nayarit: Sierra San Juan. Jalisco: La Floresta (Lago de Chapala). Queretaro: Montenegro, Tequisquiapan, Ciudad de Queretaro and 10 mi N of Ciudad de Queretaro. Hidalgo: Tasquillo, Jacala, Don Guiño, Santiago de Anaya. Guanajuato: San Miguel de Allende, Ciudad de Guanajuato, Celaya. Puebla: Matamoros, km 75 carr. Tehuacan-Huajuapan de Leon, Tehuacan. Morelos: Tepoztlan, km 83 carr. Cuernavaca-Tepoztlan, Cañon de Lobos, Cuernavaca, Las Estacas. Colima: Ciudad de Colima. Estado de Mexico: Pto. Los Gallos and 28 mi W of Toluca. Oaxaca: Ciudad de Oaxaca, Montealban, Mitla, Huajuapan de Leon, Ixtlan, Teotitlan del Valle, and km 40 carr. Oaxaca-Gelatao. Michoacan: Petatan, Acambaro, 20 km, W of Zitacuaro, Morelia, Jiquilpan, Cuitzeo. Guerrero: Rodecia, Teloloapan, Cañon del Zopilote, Estacion de Microondas Tuxpan and 11 mi N of Ixtapan de la Sal. Vera Cruz: 5 mi E of Acultzingo. Distrito Federal: Tonatico. EL SALVADOR: Puerto La Libertad.

> Thasus heteropus (Latreille)
> (Figs. 4, 14, 21, 25, 32)

Coreus heteropus Latreille, 1811:189
Redescription. Male: Color: Dorsum, antennae, dorsal surface of legs, brown to deep brown, almost black; membrane darker. Dorsum (including exposed lateral margins of abdominal terga), legs, and antennae, but not membrane, heavily beset with short, recumbent, golden setae. Venter sometimes lighter brown, especially ventral surfaces of legs. Venter sparsely beset with golden setae. Thoracic pleura each with discoidal patch of long, dense, recumbent golden setae, just lateral to subcoxae. Structure: Apical half of antennal 3 only slightly dilated, asymmetrically. Pronotal rise about $45^{\circ}$, humeral angles with small sharp tooth, lateral margins of pronotum slightly crenulate. Abdominal terga more or less exposed lateral to wings; terga 4-7 with small blunt spines apicolaterally, those on 4 and 7 very small. Rostrum nearly attaining metasternum. Hind tibial expansion without tooth; hind coxae with round protuberance; hind trochanter with small blunt spine.
Female: as male, except hind coxa and trochanter with slight round protuberances. Plica of seventh sternum with very small blunt tooth.
Measurements: Table 1.
Holotype: We have been unable to locate the holotype of this species.


Fig. 32A-C. Variation in ventral rims of Thasus heteropus genital capsules; dorsal views. A. Representing specimens from Argentina, Ecuador (small hind femora), Venezuela, no locality on label. B. Peru, Ecuador (normal hind femora, 2 specimens). C. Colombia.

Variation: Nearly all specimens examined are dark brown to near black, but a few are somewhat lighter, to light brown. In addition, the hind femora of one male from Ecuador are much less incrassate than the hind femora of other males (including several from Ecuador); its hind femora however are more incrassate than those of any female. Males vary also in the size and shape of the genital capsule's ventral rim: in some the median excision is deeper than in others; and the lobes lateral and interior to the edges of the excision vary in shape (Fig. 32). The capsule of the Ecuador male with small hind femora differs from those of two Ecuador specimens with "normal" hind femora (Fig. 32A, B). The seventh connexival segment of the female may have or lack a tiny lateral spine.
Diagnosis: This species has the third antennal entirely black, with the dilated portion narrow and elliptical (Fig. 14). Claval and corial veins are unicolorous with the corial surface. For other features, see under T. odonnellae.
Distribution: COLOMBIA: Bogota, Nova Granada. ECUADOR: Santa Cecilia (Dallas, 1852; Froeschner, 1981; Stål, 1870; Walker, 1871).

New records: COLOMBIA: Santa Elena, Gigante (Huila Prov.), "de Savannah de Bogota." ECUADOR: Alóao, Balzapamba, Chiriboga, Interandins, LaVega, Portoviejo, Rio Toachi. PERU: Chanchamayo. VENEZUELA: Carbonera, Mucuruba.

Thasus luteolus, Brailovsky \& Barrera, n. sp.
(Figs. 5, 15, 26)
Description. Male: Color: Head including antennals 1-4 black, yellow between ocellus and eye. Pronotum reddish-brown, anterior margin, anterolateral edge, posterior margin black, posterolateral margin and spine of humeral angle pale yellow, callus with two orange irregular spots on each side of midline. Scutellum bright reddishbrown, with apex black and lateral edge pale yellow. Clavus and corium reddishbrown with following areas pale yellow: claval and corial veins, claval commissure, posterior half of anal edge, costal margin, apical angle, apical margin of corium. Hemelytral membrane chestnut brown, basal angle and veins darker. Connexival segment 2 entirely black, 3 and 4 black with anterodorsal edge yellow, 5-7 with anterior third yellow and the rest including the spines black; abdominal terga black. Ventrally, head and rostral segments black; prosternum black, mesosternum black with median discoidal orange spot, metasternum orange with anterior and lateral edges black; propleuron black with two orange spots, one near acetabulae, the other running below anterolateral edge. Mesopleuron orange with external and inferior margins black; metapleuron orange with posterodorsal angle black. Anterior lobe of metathoracic scent gland dirty yellow, posterior lobe and neighboring areas black. Fore and middle acetabulae black, with an elongate orange spot; posterior acetabulae orange with superior, external, and inferior edges black. Coxae bright orange with inferior edge black; trochanters black laterally, bright orange medially. Fore and middle femora black, with two orange rings, one basal, the other subdistal; posterior femora reddish-brown basally, an incomplete subdistal ring orange; fore and middle tibiae black with medial yellow spot; external dilation on posterior tibiae black with elongate yellow spot near middle, internal dilation with anterior half yellow and posterior half black and with elongate yellow spot near middle; tarsi black. Abdominal sternites bright orange, posterior edge of sternum 7, spiracles black. Pleural margin 2 entirely black, 3-7 with anterior margin or anterior half yellow and the rest including spines black. Structure: Dilation of third antennal segment narrowly elliptical to lanceolated in outline. Anterolateral border of prothorax with small spines to nodulose; humeral angles wider, relatively exposed, with slight spine. Posterior tibiae dilated, lanceolate, inner dilation with broad spine. Posterior angles of connexival segments 4-7 with large spine. Posteroventral border of genital capsule with four short extensions, lateral ones robust and slightly exposed, middle ones quadrate and a small concave space between.
Female: Color: Similar to male. Posterior tibiae black with elongate yellow spot on external dilation and on internal dilation. Connexival segments 8 and 9, and abdominal terga 8 and 9, black. Gonocoxa 2 black with orange red spot on external angle, another on middle basal side. Paratergite 8 black; paratergite 9 orange with upper edge dark brown. Spermatheca: Figure 26. Structure: Posterior tibiae dilated and lanceolate, margins entire; posterior angles of connexival segments 4-6 each with small spine, segment 7 truncate without spine.
Measurements: Table 1.

Variation: 1. Mesosternum, metasternum, and acetabulae entirely black. 2. Fore and middle trochanters almost black. 3. Fore and middle femora black, with two incomplete and diffuse dirty orange rings. 4. Abdominal sternum black with anterior half lateral to middle line dark orange red. 5. Gonocoxae 1 black with external and basal margin yellow. 6. Paratergite 8 black with a median and internal yellow spot.
Holotype: Male. COSTA RICA: Provincia San Jose: Uruca, 13.XII. 1981, L. Alvarez. Deposited in IBUNAM.
Paratypes. One female: COSTA RICA: Provincia Cartago: Orosi, 20.I. 1980, Helga Blanco. Deposited in UCCR. One female: COSTA RICA: Provincia Cartago: El Llano, 1.VII. 1983, Fdo. Vazquez. Deposited in IBUNAM.
Diagnosis: Like T. heteropus, T. luteolus has the second antennal entirely black, and its dilation small (Figs. 14, 15). In T. luteolus, connexival segments 4-7 are black with an anterior yellow spot, clavus and corium with pale yellow veins, contrasting with the brown red surface, tibiae black with middle yellow spot, and pronotum slightly declivent. In T. heteropus, the connexival segments and tibiae are entirely brown to brown-orange or black, the clavus and corium (including veins) are unicolorous, and the pronotum is more declivent.
Etymology. Named for the yellow spot on the tibiae.
Thasus neocalifornicus, Brailovsky \& Barrera, n. sp.
(Figs. 6, 13, 27)
Pachylis gigas: Uhler, 1875:831 (misidentification)
Pachylis gigas: Uhler, 1876:295 (misidentification)
Pachylis gigas: Uhler, 1877:1325 (misidentification)
Thasus gigas: Distant, 1881:108 (partial misidentification)
Pachylis gigas: Uhler, 1886:10 (misidentification)
Pachylis gigas: Uhler, 1894:232-233 (misidentification)
Thasus gigas: Van Duzee, 1917:92-93 (misidentification)
Thasus gigas: Van Duzee, 1923:132 (misidentification)
Thasus acutangulus: Torre Bueno, 1940a:45 (misidentification)
Thasus gigas: Torre Bueno, 1940b:102 (misidentification)
Thasus acutangulus: Torre Bueno, 1941:54 (misidentification)
Thasus gigas or acutangulus ?: Torre Bueno, 1942:184 (misidentification)
Thasus acutangulus: Torre Bueno, 1945:83 (misidentification)
Thasus gigas: O'Shea, 1980:219 (partial misidentification)
Thasus acutangula: O'Shea, 1980:219 (partial misidentification)
Description. Male: Color: Head shiny black, space between ocellus and eye dark orange. Antennal 1 shiny black, 2 shiny black with bright reddish reflections on basal third, 3 bright orange with dilated area shiny black, 4 dull orange red. Pronotum, scutellum bright brown to black, with reddish reflections. Clavus, corium dark brown, with following areas pale yellow: claval and corial veins, apical third of anal border, claval commissure, costal margin, apical angle, apical margin, and a few scattered spots between corial veins; membrane brown amber with veins and basal angle darker. Connexival segments 2-4 dark reddish-brown, segments 5-7 bicolored, anterior third or anterior half bright orange red and posterior half dark brown red, always with spines and superior margin shiny black. Abdominal terga bright orange red, posterior
half of segment 7 dark brown red. Head dull orange ventrally, bucculae and rostral segments dark brown red. Pleuron dark brown red, with three or four bright red orange areas, one or two on propleuron and one each on mesopleuron and metapleuron. Anterior and posterior lobes of metathoracic scent gland black with dark orange reflections. Coxae bright orange, apical third shiny black; trochanters black with bright orange reflections; femora black with two bright orange-red rings, one basal, the other near apical third; tibiae black with two bright orange-red incomplete rings, one near basal third, other near apical third; tarsi shiny black. Abdominal sterna dark orange red, posterior third or posterior half mostly black; pleural margins $2-4$ orange red and $5-7$ with anterior third or anterior half, orange red, the rest (including dorsal border and spines) black. Genital capsule black, laterally dark orange red. Structure: Dilation of antennal 3 broad, obovate, foliate. Pronotum conspicuously declivent, inclination $50^{\circ}-56^{\circ}$; anterolateral border with small spines; humeral angles exposed, apex somewhat projected as a spine. Posterior tibiae slightly dilated and lanceolate, inner dilation with broad spine. Posterior angles of connexival segments 4-7 with small to large spines. Posteroventral border of genital capsule with four long arms, lateral ones broad, quadrated, and apically truncated, middle ones shorter and globose, and large medial straight space between.
Female: Color: Similar to male. Connexival segment 8 black, 9 bright orange red with posterior angle black; abdominal terga 8 and 9 with anterior half bright orange red and posterior half black; gonocoxae 1 and paratergite 8 black with basal third bright orange red; paratergite 9 with anterior half bright orange red and posterior half black.
Structure: Posterior tibiae slightly dilated and lanceolated, all margins entire; posterior angles of connexival segments 4-7 with small to large spines. Spermatheca: Figure 27. Measurements: Table 1.
Variation: 1. Antennal 2 black with basal third bright orange red. 2. Antennal 3 black. 3. Antennal 4 dark orange, or pale brown orange, or mottled with dark brown. 4. Trochanters bright orange red. 5. Anterior lobe of metathoracic scent gland dirty ochre. 6. Pleura uniformly dark brown red. 7. Abdominal sternites, including pleural margins and genital plates of female, bright pale red and with only superior border and spines shiny black. Note: In very dark specimens, the banding of the tibiae and femora may be obscured, as may be other areas where, in paler specimens, yellow or orange occurs. Indeed, we have two specimens collected on the same day at the same place in Arizona; one has the banding and the other, much darker, does not. Holotype: Male. MEXICO: Baja California Sur: km 75.5 carr. La Paz-San Jose del Cabo, 11.IX. 1977, R. Lopez. Deposited in IBUNAM.
Paratypes. Two males and three females. Same data as holotype. Deposited in CAS, TAMU, IBUNAM. Two males, one female: MEXICO: Baja California Sur: Todos Santos, 5.VIII. 1984, A. Martinez. Deposited in IBUNAM. Four males, two females: MEXICO: Baja California Sur: 15 km , SE de El Triunfo, 15.VII. 1982, E. Barrera and H. Brailovsky. Deposited in AMNH, BMNH, and IBUNAM. One male: MEXICO: Baja California Sur: Mulege, 12.VIII. 1981, E. Barrera. Deposited in IBUNAM. Three males, three females: MEXICO: Baja California Sur: km 75 carr. Cabo San Lucas-La Paz, 11.IX. 1977, M. Santamaria. Deposited in AMNH, CAS, USNM, IBUNAM. One female: MEXICO: Baja California Sur: La Paz, 10.IX. 1959, D. R. Estes. Deposited in FSCA. Two males, one female: MEXICO: Baja California Sur:

1 km east of E. Triunfo (533 m), 27.VII. 1974, R. M. Haradon, W. E. Savary, V. F. Lee. Deposited in UCB. One male: MEXICO: Baja California Sur: La Paz (Hotel Guaycura), X.1929. Deposited in CMP. One female: MEXICO: Sonora: Santa Ana, 3.XI. 1986, F.Arias. Deposited in IBUNAM. Two females: UNITED STATES: Arizona: Pima Co., Tucson, 29.VII. 1969. Deposited in FMNH. One male: UNITED STATES: Arizona: Santa Cruz Madera, without data. Deposited in FSCA. Two males, two females: UNITED STATES: Arizona: Cochise Co., 7 mi W, Benson, 1.IX. 1968, J. B. Heppner. Deposited in FSCA. One male: UNITED STATES: Arizona: Santa Cruz Co., Peña Blanca Cyn., (4,200 ft) 1.VIII. 1974, S. Szerlip. Deposited in UCB. Four males and one female: UNITED STATES: Arizona: Pima Co., Florida Cn., 3. VIII. 1983, S. Ziff. Deposited in LACM and IBUNAM.

Discussion: There has been uncertainty in the literature over the species of Thasus occurring north of Mexico. Uhler reported Pachylis gigas for this region (1875, 1876, 1877, 1886, 1894), and this was followed by Van Duzee (1917, 1923). In 1940 (a), Torre Bueno reported Thasus acutangula from Arizona, but later in that year (1940b), using notes from Barber, he changed his identification to Thasus gigas. Later (1941), he listed T. acutangula from Arizona and New Mexico and rejected T. gigas as probably a misidentification; the following year Torre Bueno (1942) expressed doubts about Van Duzee's (1923) use of gigas and suggested acutangulus. O'Shea (1980) listed both forms from the United States without any clarifying comment. Recently, Froeschner (1988) referred again to the subject and discussed it briefly; he decided to conserve T. gigas as probably the North American species.

Examining the extensive collection of Thasus housed in IBUNAM as well as much material from other American collections, we (H.B. and E.B.) realized that a new species, closely related to the other two, was involved. This new species is distributed in the northwest of Mexico, and in Arizona and New Mexico. The other two species (T. gigas and acutangulus) are more southern.

Thasus neocalifornicus is more closely related to T. gigas (Burmeister) and $T$. acutangulus (Stål), sharing the antennal segment 3 obovate, conspicuously dilated, foliate, and bicolored (Figs. 9, 12, 13).

The following combination of characters will serve to separate $T$. neocalifornicus from T. gigas: body large and relatively slender, antennal 4 dull orange red and shorter (usually under 6.20 mm ), humeral angles exposed, with apical spine somewhat pointed, ventral head dull orange, maximal width of abdomen less than 12.30 mm , antennal 2 bicolored, pronotum much declivent $\left(50^{\circ}\right.$ to $\left.56^{\circ}\right)$. In $T$. gigas the body is large and broad, antennal 4 brown or black (but sometimes reddish-brown) and larger (usually above 6.30 mm ), humeral angles obtuse and rounded, ventral head black, maximal width of abdomen above 13.00 mm , antennal 2 entirely black, and pronotum barely declivent ( $45^{\circ}$ to $50^{\circ}$ ).

The females of $T$. neocalifornicus and $T$. gigas are alike in color of femora and tibiae and development of the ventral and dorsal dilation of the posterior tibiae, whose maximal width is usually less than 2.75 mm ; and the posterior angles of their connexival segments 7 have a long spine.

In T. acutangulus the maximal width of the posterior tibiae is usually more than 2.80 mm , and the posterior angle of the female's connexival segment 7 is truncated, without a spine. The bicolored antennal 2 and the remarkably declivent pronotum ally T. neocalifornicus and T. acutangulus. The following combination of characters
will serve to separate these species. In $T$. neocalifornicus, antennal 4 is dull orange red and shorter (usually under 6.20 mm ) and femora and tibiae have orange red rings. In T. acutangulus antennal 4 is brown to black and larger (usually above 7.20 mm ); width of abdomen above 13.85 mm ; and the femora and tibiae are entirely black or bright orange, with the anterior and posterior third black and without orange rings.

Finally, this is the only species of Thasus (or, as far as we know, of Pachylis) in which antennals 3 and 4 are subequal; in all other species, 4 is longer than 3 (Table 1). This character (subequality of 3 and 4 ) does not appear to vary.

Etymology: Named for its occurrence in the Baja California Region.
Biology: Jones (1993) gives the most complete account available of the biology of this species (in several localities in Arizona). Eggs are laid in chains of a dozen or so, concealed in or under stems and loose bark of the host plant, the legume velvet mesquite (Prosopis velutina Woot.). All instars are gregarious.

Thasus odonnellae, Schaefer \& Packauskas, n. sp.

(Figs. 7, 16, 17, 22, 28)
Description. Holotype male: Color: Dorsum, antennae, brown; legs deep red-brown; membrane darker. Dorsum (including exposed lateral margins of abdomen) heavily beset with short recumbent golden setae, these heavily concentrated along lateral margins of prothorax. Venter deep red-brown, the following areas dark brown to black: auricle of metathoracic scent gland, base of coxae, apex of femur, rostral 4, spines of hind tibia and of abdominal segments, incomplete irregular medial stripe on metasternum. Spiracles narrowly ringed with yellow. Venter lightly beset with golden setae. Thoracic pleura each with discoidal patch of long, dense, recumbent, golden setae, just lateral to subcoxae. Structure: Apical two-thirds of antennal 3 moderately dilated, asymmetrically. Pronotal rise about $50^{\circ}$; anterior half of lateral margins of pronotum smooth; posterior half with several very small teeth; humeral angles blunt. Abdominal terga narrowly exposed lateral to wings; terga 4-7 with small sharp spines apicolaterally. Hind tibial expansion with median tooth. Hind coxa and trochanter each with blunt fingerlike protuberance, that of trochanter smaller. Paramere: Figure 21.
Paratype female: As male, except more heavily beset with golden setae both dorsally and ventrally, except pronotal collar and calli nearly bare; scent gland auricle, coxal spine red-brown (concolorous with venter), and without medial metasternal stripe. Spiracles not ringed with yellow. Abdominal terga more broadly exposed laterally. Without spines on hind tibia and trochanter, hind-coxal protuberance slight. Plica of seventh sternum with small blunt spines. Spermatheca: Figure 25.
Measurements: Table 1.
Diagnosis: Most similar to $T$. heteropus, from which it differs in the greater development of both the antennal and the hind-tibial dilations, and of the hind-tibial, abdominal tergal, and plical spines; the more blunt humeral angles; the heavier coating of golden setae (especially in the female); the generally lighter coloration (although some T. heteropus are as light as T. odonnellae, and other specimens of the latter may prove to be darker than these types).
Type locality: BOLIVIA: Rio Cristal Maru.
Label data: holotype male: label 1) Rio Cristal Maru $50 \mathrm{mi} /$ NE Cochabamba, Bolivia/

X-15-1949/ Collector: A Pena. 2) J. C. Lutz/ Collection/ 1961. Right antenna pointmounted separately on pin; genitalia in vial on pin. Paratype female: 1) same, except X-31-1949. 2) Same. Both specimens in NMNH.
Variation: We have a third specimen of this species, a female (from CU) lacking any locality information. This female has the black auricle and yellow-ringed spiracles of the holotype male; the paratype female lacks both these features.
Etymology: This species is named for Dr. J. E. O’Donnell, in recognition of her contributions to the study of Heteroptera, and of her aid to entomologists as curator of the University of Connecticut Insect Collection.

Thasus rutilus, Brailovsky \& Barrera, n. sp.
(Figs. 8, 11, 29)
Description. Male: Color: Dorsum dark reddish-brown, with anterolateral edge of pronotum and transverse ridge of pronotal disk darker and following areas dark orange ochre: space between ocellus and eye, lateral edge and apex of scutellum, claval and corial veins, claval commissure, costal margin, apical angle and apical margin of corium. Antennals 1 and 2 entirely black, 3 and 4 bicolored, with anterior half pale orange yellow and posterior half black. Hemelytral membrane dark ambarine, with basal angle and veins darker. Connexival segment 2 entirely pale orange yellow, 3 reddish-brown with superior edge pale orange yellow, 4-7 reddish-brown with shiny black spines. Abdominal terga 1-6 pale orange red, 7 orange red with a central black spot. Venter pale chestnut orange. Rostral segments 1-3 dark chestnut orange, 4 black. Pleural margins of abdominal sternum 2 entirely pale yellow, 3 pale chestnut orange with central yellow spot, 4-7 pale chestnut orange with lateral edges and spines black. Coxae and trochanters pale chestnut orange with bright red reflections; femora pale orange red, with apical edge black; tibiae dark orange with subdistal third black or darker; tarsi pale orange. Structure: Dilation of antennal 3 broadly obovate and foliate. Anterolateral border of pronotum nodulose; humeral angles broadly exposed, ending in obtuse spine. Posterior tibiae dilated, lanceolate, inner dilation with large spine. Posterior angles of connexival segments $4-7$ each with large spine. Posteroventral border of genital capsule with large bilobated medial plate, laterally delimited by short and globose projection.
Female: Color: Similar to male. Connexival segments 8 and 9 and abdominal terga 8 and 9 reddish-brown; black central spot on tergum 8; posterior edge of tergum 9 black. Genital plates entirely pale chestnut orange. Structure: Posterior tibiae slightly dilated and lanceolate, both inner and outer margins entire. Posterior angle of connexival segments 4-7 each with large spine. Spermatheca: Figure 29.
Measurements: Table 1.
Variation: 1. Connexival segments 3-9 bright orange red, dorsal border and spines black. 2. Abdominal terga 1-6 bright orange yellow. 3. Ventral surface pale orange yellow with acetabulae chestnut orange.
Holotype. Male. BRAZIL: Mato Grosso: Sinop, X. 1976, M. Alvarenga. Deposited in CMP.
Paratypes. Nine males, twelve females. Same data as holotype. Deposited in CMP and IBUNAM. One male: BRAZIL: Mato Grosso: Diamantino, Facienda Sao Joao ( 450 m ), 8.II. 1981, G. Ekis. Deposited in CMP. Two males: FRENCH GUIANA: Mana River, X. 1917 (acc. 6008). Deposited in CMP. One female: PERU: Madre
Table 2. Character states, polarities, and distributions of Thasus and Pachylis.

| Character | T. acutangulus | T. gigas | T. neocalifornicus | T. heteropus | T. odonellae |
| :---: | :---: | :---: | :---: | :---: | :---: |
| a. Metatibial dilation | symmetrical (1) | symmetrical (1) | symmetrical (1) | symmetrical (1) | symmetrical (1) |
| b. Pale hirsute spots on pleura | absent (2) | absent (2) | absent (2) | large (1) | large (1) |
| c. Female connexival VII spine | absent (0) | present (1) | present (1) | present (very small) <br> (1) | present (1) |
| d. Antennal III dilation | symmetrical (1) | symmetrical (1) | symmetrical (1) | asymmetrical (0) | asymmetrical (0) |
| e. Antennal III dilation | large (0) | large (0) | large (0) | small (1) | small (1) |
| f. Humeral angle | sharp (1) | rounded (0) | sharp (1) | sharp (1) | subacute (0) |
| g. Metatrochanter spine | small (1) | large (0) | large (0) | small (1) | small (1) |
| h. Female sternum VII spine | absent (0) | present (1) | present (1) | present (very small) <br> (1) | present (1) |
| i. Second valvula tooth | broadly rounded $\left(1^{\mathrm{a}}\right)$ | asymmetrically bifid, both tips rounded (2) | broad, slight median indentation <br> (2) | obtuse ( $1^{\text {b }}$ ) | sharp (0) |
| j. Corial veins | dark (0) or bright $\left(1^{\mathrm{a}}\right)$ | bright (1a) | bright (1a) | dark (0) | dark (0) |
| Distribution | Mexico, no. Central Amer. | Mexico, Central Amer. | no. Mexico, s.w. U.S. | no. S. Amer. | Bolivia |

Table 2. Extended.

| T. Iuteolus | T. carchinus | T. rutilus | P. laticornis | P. pharaonis | P. spp. |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $\begin{aligned} & \text { symmetrical (1) } \\ & \text { absent ( } 2 \text { ) } \end{aligned}$ | symmetrical (1) absent (2) | symmetrical (1) large (1) | $\begin{aligned} & \text { asymmetrical (0) } \\ & \text { tiny (0) } \end{aligned}$ | $\begin{aligned} & \text { asymmetrical (0) } \\ & \text { tiny (0) } \end{aligned}$ | $\begin{aligned} & \text { asymmetrical (0) } \\ & \text { tiny (0) } \end{aligned}$ |
| absent (0) | present (1) | present (1) | absent (0) | absent (0) | absent (0) |
| asymmetrical (0) | symmetrical (1) | asymmetrical (0) | asymmetrical (0) | asymmetrical (0) | asymmetrical (0) |
| small (1) | large (0) | large (0) | large (0) | large (0) | large (0) |
| rounded (0) | sharp (1) | subacute (0) | rounded (0) | subacute (0) | rounded (0) |
| large (0) | ? | small (1) | large (0) | large (0) | large (0) |
| absent (0) | ? | present (0) | present (0) | present (0) | present (0) (absent in one specimen) |
| broadly rounded ( $1^{\text {a }}$ ) | ? | obtuse ( $1^{\text {b }}$ ) | sharp (0) | sharp (0) | sharp (0) |
| bright ( ${ }^{\text {a }}$ ) | bright ( $1^{\text {a }}$ ) | dull yellow ( ${ }^{\text {b }}$ ) | dark (0) | yellow (1 ${ }^{\text {b }}$ ) | yellow ( $1^{\text {b }}$ ) |
| Costa Rica | Ecuador | Brasil, Fr. Guiana | Pachylis: Mexico sout | Argentina; mostly | mer. (O'Shea, 1980) |

de Dios: Rio Rambopata Res., 30 km (air) SW of Pto. Maldonado ( 290 m ), $12^{\circ} 50^{\prime} \mathrm{S}$, $69^{\circ} 20^{\prime}$ W, 17.II. 1982, R. Wilkerson. Deposited in FSCA.
Diagnosis: This new species is very distinctive: antennals 3 and 4 bicolored, connexival segment 2 entirely pale orange yellow and contrasting with the reddish-brown of segments 3-9.

In T. heteropus, antennals 3 and 4 are entirely black, the dilated portion of segment 3 is narrow and elliptical (Fig. 4), and connexival segments 2-9 are dark brown to black. T. gigas has antennal 2 entirely black (Fig. 3), but the humeral angles are rounded and obtuse, antennal 4 is black or dark brown and shorter (under 8.25 mm ), and connexival segments $2-9$ are dark brown to black with scatterd yellow spots. Etymology: Named for the yellow to pale orange yellow connexival segment 2.

## PHYLOGENY

## Discussion of characters (Table 2)

Characters a-c.-An asymmetrical metatibial dilation (a), a spineless female seventh connexivum (b), and thoracic pleura with very small hirsute patches (c) all occur in the sister genus, Pachylis, and are considered plesiomorphic. All Thasus have a symmetrical or nearly symmetrical tibial dilation. None has small pleural patches, but some have large ones and others have none. We believe the progression small $\rightarrow$ large $\rightarrow$ none to be more likely than small $\rightarrow$ none $\rightarrow$ large. A seventh connexivum without a spine occurs in the females of two species of Thasus (Table 2); we believe this condition represents independent secondary losses, and therefore treat it as an apomorphy over the presence, which is plesiomorphic within Thasus but an autapomorphy of the genus relative to Pachylis.
Characters d-i.-The states we consider plesiomorphic occur in all Pachylis studied, and in some Thasus. Different states in Thasus, we consider apomorphic. One character requires further discussion: The tip of the female's second valvula bears a well sclerotized broadly flattened tooth, which is sharply pointed in Pachylis. It is either obtuse or broadly rounded in Thasus (except in T. odonnellae, where it is sharp, a reversal). In T. neocalifornicus it is depressed medially, and in T. gigas it is asymmetrically bifid. We treat the sharp condition as plesiomorphic, and suggest two pathways therefrom: sharp $\rightarrow$ broadly rounded (condition $1^{\text {a }}$ ) $\rightarrow$ slightly or asymmetrically bifid (2); and sharp $\rightarrow$ obtuse ( $1^{\mathrm{b}}$ ).
Character j. - The veins of the corium of Thasus may be dark (concolorous with the corium itself), bright yellow or orange, or dull yellow (T. rutilus). The last two occur also in Pachylis and, indeed, in other genera of Nematopodini. The first two conditions occur within T. acutangulus, in specimens both dark and light; therefore corial color does not seem correlated with overall darkness of the specimen, as does variation in banding of the legs. Because dark and bright occur intraspecifically, yellow coloration seems not to be intermediate. Therefore we postulate two advanced states, bright ( $\mathrm{j}^{\mathrm{a}}$ ) and yellow ( $\mathrm{j}^{\mathrm{b}}$ ) corial veins, each derived directly from dark veins.

## Phylogeny (Fig. 33)

Two clades are apparent. T. odonnellae + (rutilus + heteropus ) is characterized by a small dilation of antennal 3 and a small metatrochanteral spine; each of these apomorphies occurs homoplasiously in the second clade, but not together. In this


Fig. 33. Cladogram of species of Thasus. Most terminal autapomorphies omitted. ${ }^{*}=$ convergence. ${ }^{* *}=$ reversal.
first clade the corial veins are concolorous with the corium itself, except in T. rutilus, where they are yellow, but not so bright as in the second clade. Otherwise, these species are uniformly brown (except for the hirsute patches on the pleura).

Members of the second clade (the other five species) have lost the pale hirsute patches on the pleura, their females have a broadly rounded tooth on the second valvula, their corial veins are contrastingly bright, and all but carchinus and acutangulus have orange or yellow markings on their legs.

Thasus carchinus is suggested here to be the sister genus of T. acutangulus. However, we do not know the states of several characters for this species (Table 2), and so its position in the cladogram is unsure. We predict that T. carchinus will have a large metatrochanteral spine (character g); but we cannot predict its states of characters $h$ and $i$.

Finally, the facts that $T$. neocalifornicus has the northernmost distribution of the genus, and is the only Thasus (or Pachylis, as far as we know) whose antennals 3 and 4 are subequal, suggest to us that this is the most advanced-the most recently arisen-species in the genus.

## DISTRIBUTION

The T. odonnellae + (rutilus + heteropus $)$ clade is the southernmost in Thasus; and it also shares more features (Fig. 33) with the predominantly South American (O'Shea, 1980) Pachylis than do the other Thasus species (except T. luteolus). The other five Thasus species extend from the southwestern United States through Central America; only one is South American, T. carchinus, in Ecuador.

The range of the first Thasus clade overlaps that of Pachylis more than does that of the second clade (Pachylis range in O'Shea, 1980), but the distributions of four of the ten Pachylis species are unknown; and indeed several Pachylis extend into Central America and one ( $P$. hector Stål) occurs in México.

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# ETAPOCANGA, A NEW GENUS AND TWO NEW SPECIES OF NEOTROPICAL FLEA BEETLE (COLEOPTERA: CHRYSOMELIDAE: ALTICINAE) 

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Abstract.-A new genus, Etapocanga, and two new species of Alticinae (Coleoptera: Chrysomelidae), Etapocanga pysuna and Etapocanga consejera from Amazonian South America are described and illustrated.

Resumen.-Se describe y illustra un nuevo género, Etapocanga, y dos especies nuevas de Alticinae (Coleoptera: Chrysomelidae) de América amazónica.

While preparing a monograph of genus Pedilia Clark, 1865, I encountered material of a new genus in the flea beetle tribe Disonychini. This genus could be confused with Pedilia Clark because of its asymmetrical and highly emarginate eye or less likely with Paralactica Bechyné and Bechyné, 1961. Paralactica is superficially similar to this genus, because of its elongate habitus, comparatively large size and fulvousness. In Paralactica, however, the eyes are symmetrically emarginate, the emargination taking the form of a notch (Bechyné and Bechyné, 1977, their fig. 3).

This genus is easily distinguished from Monomacra Chevrolat, 1837, Parchicola Bechyné and Bechyné, 1975, and Ultingaltica Bechyné and Bechyné, 1961 because of its eye shape (see Fig. 2). It is also distinguished from Disonycha Chevrolat, 1837 and Phenrica Bechyné, 1959 by the presence of a prebasal pronotal impression (see Fig. 1).

This new genus is described below so it may be included in a phylogenetic analysis of the tribe Disonychini in a manuscript in preparation.

Terminology used to describe the dorsal process of the median orifice of the aedeagus is taken from Duckett (1993).

## Etapocanga, new genus

(Figs. 1, 2, 3A-G)
Type species. Etapocanga pysuna, new species.
Diagnosis. Etapocanga is distinguished from Pedilia by pronounced transverse prebasal pronotal impression, long gracile antennae and less extremely incrassate metafemora and from all other Neotropical genera by the asymmetrical emargination of the eye (Fig. 2).
Description. Body robust, broadly ovate, convex, $6.8-7.6 \mathrm{~mm}$ long, $4.0-4.4 \mathrm{~mm}$ wide at elytral midpoint (Fig. 1), color uniformly fulvous: mandibles and antennae piceous.

[^6]

Fig. 1. Etapocanga pysuna, dorsal habitus.

Head ovate (Fig. 2), occiput broader than eye at widest point; vertex glabrous, one post-ocular seta. Eye emarginate, upper lobe slightly smaller than lower lobe (see Fig. 2). Post-antennal calli distinct, trapezoidal, delimited on three sides by sutures. Transverse frontal carina pronounced, convex, widened over labrum, extending to mandibular bases; transverse carina confluent with longitudinal frontal carina; longitu-


Fig. 2. Head of Etapocanga pysuna, antennae removed.
dinal carina convex, extending between the antennal sockets, dorsally delimited by suture. Clypeus and labrum transverse. Labrum with dense row of apical bristles. Mandible with four teeth. Maxillary palpus robust, penultimate segment slightly incrassate.

Antenna long, filiform, sparsely pubescent, extending beyond elytral midpoint; antennomere II the shortest element, sub-trapezoidal; antennomere III wider apically than basally; antennomeres IV-X cylindrical, $3-4 \times$ longer than wide; XI with subapical constriction, antennomere appearing annulated.

Pronotum glabrous, transverse, convex, width at base $2 \times$ length, anterior angles rounded and abutting posterior margin of eyes, with seta on posterior edge of anterior angle, setal pit prominent; pronotal lateral margins distinct, narrow, accompanied by single row of punctures one antennal width (antennomere VI) mesad of margin. Posterior angles minute, directed posteriorly. Prebasal impression narrow, clearly


Fig. 3. Etapocanga genitalia. A, E. pysuna median lobe, dorsal view, B, lateral view. C, E. consejera median lobe dorsal view, D, lateral view. E, E. pysuna spermatheca. F, E. pysuna sternite VIII, ventral view, G, lateral view. MDP = Median dorsal process, LDP = Lateral dorsal process, IPIM = Insertion point of intersegmental membrane.
delimited laterally and anteriorly (see Fig. 1). Elytra combined slightly wider than pronotal base; humeral callus indistinct; elytral punctuation confused. Elytral margin narrow; epipleuron horizontal, wide at humerus gradually narrowing, becoming obsolete near elytral apex. Scutellum triangular, glabrous.

Prosternum with anterior angle abutting ventral lobe of eye; anterior portion of prosternum broader than one antennal width, without sculpturing; prosternal process extending beyond procoxal cavities, narrowing between coxae, widening posteriorly. Procoxa round. Procoxal cavity open. Mesosternum slightly excavated anteriorly to receive prosternal process, narrow posteriorly, posterior edge sharply notched. Mesocoxa round. Metasternum long, broad, finely pubescent. Metacoxa narrow, transverse, tapered laterally. Leg robust; metafemur incrassate; metatibia bearing short apical spur, small apical lateral comb present; tarsi broad, broadest in males, tarsomere III bilobed; claws appendiculate.

Abdomen finely pubescent. Pygidium formed from tergum VIII, rounded.
Male genitalia (Fig. 3A, B) with median lobe elongate, tubular, with three processes dorsal to medium orifice. Ventral lip of median lobe triangular, widest near midpoint of dorsal processes. Median dorsal process narrow, apex in same plane. Lateral dorsal process width variable, apex recurved medially. Endophallus with microtrichia.

Female genitalia with epiproct, gonapophyses and gonocoxae absent. Sternite VIII with apex broad; attachment of intersegmental membrane pointed; broad basally, basal edge flat (Fig. 3F) spoon-shaped in lateral view (Fig. 3G). Spermatheca (Fig. 3 E ) with curved parallel-sided pump; receptacle ovate, with prominent ridges for insertion of spermathecal muscle; proximal spermathecal duct expanded.
Distribution. Amazonian Brazil and Venezuela.
Etymology. From Tupí, a language indigenous to Amazonian Brazil, Etapocanga meaning rare.

Etapocanga pysuna, new species
(Figs. 1, 2, 3A, B, E-G)
Diagnosis. E. pysuna is distinguished from E. consejera by piceous tarsi. Males are also distinguished by the very narrow lateral dorsal process of the median lobe of aedeagus.
Description. Body elongate oval (Fig. 1), 6.8-7.6 mm long, 4.0-4.4 mm wide, color fulvous, mandibles, antennae and tarsi piceous, lateral apices of tibiae darkened.

Head with pronounced longitudinal frontal carina, widened above labrum. Antenna with antennomere I fulvous laterally, antennomere III shorter than IV; antennomeres VIII-XI very delicate.

Pronotum, elytron and venter as in generic description.
Male genitalia (Fig. 3A, B) elongate, thin, with ventral lip triangular, apex with minute median projection. Median dorsal process thin, apex pointed with slight apical broadenings. Lateral dorsal process thin, apices recurved medially.

Female genitalia with sternite VIII broad apically, apex slightly sinuate, with narrow apical ridge; insertion point of intersegmental membrane pointed; base wide; posterior edge flat (Fig. 3F). Spermatheca (Fig. 3E) with pump curved, receptacle ovate with ridges in lower half; proximal spermathecal duct broad at receptacle, short, narrowing gradually to gland valve.

Distribution. Amazonia and Río Javary.
Holotype. ô BRAZIL: Amazonas, Benj. Constant, Río Javary, xi. 1960, Dirings., (MZUP).
Paratype. $\ddagger$ Amazonas, 67-56, Baly coll. (BMNH).
Etymology. From Tupí, py, meaning foot, and suna, meaning black.
Etapocanga consejera, new species
(Fig. 3C, D)
Diagnosis. This species can be distinguished from E. pysuna by fulvous tarsi and by the widened apex of the median dorsal process of the median lobe and wider lateral process of the aedeagus.
Description. Body elongate oval (see Fig. 1) 7.0 mm long, 4.0 mm wide, color fulvous; mandibles and antennae piceous.

Head with frontal carina robust. Antenna with antennomeres I and XI fulvous; antennomere III shorter than IV; antennomeres VIII-XI delicate.

Pronotum, elytron and venter as in generic description.
Male genitalia (Fig. 3C, D) with ventral lip triangular. Median dorsal process thin, apex truncated, slightly broadened. Lateral dorsal process wider than tegmen; apices recurved medially.

Female unknown.
Distribution. Known only from the type locality.
Holotype, ô, VENEZUELA: Territorio Federal Amazonas, Occamo 13.iv.1965, F. Fernandez Y. (MIZA).
Etymology. From the Spanish, consejera, meaning counselor or teacher, in recognition of the formative influence of the collector, Francisco Fernandez Yepez, on Venezuelan entomology and entomologists.

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# DESCRIPTION OF THE LARVA OF AN UNIDENTIFIED SPECIES OF CERATOPUS SCHOENHERR, WITH COMMENTS ON PLANT ASSOCIATIONS IN CERATOPODINAE (COLEOPTERA: CURCULIONIDAE) 

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#### Abstract

The larva of an unidentified species of Ceratopus Schoenherr is described, and important structural features are illustrated. Larvae of Ceratopus have been collected repeatedly, and reared, from the fruits of species of Ficus (Moraceae) in Middle America. This represents the first larval description for a member of the subfamily Ceratopodinae. Known plant associations for this subfamily are summarized.


The Ceratopodinae (Ceratopinae auct.) are one of the smaller subfamilies of Curculionidae. In the most recent world catalog (Klima, 1935), eight genera and 22 species were recognized. Since that time a number of genera have been transferred to other subfamilies and a number of new species have been described. It appears that six genera (Aetiomerus Pascoe, Anthomelus Hustache, Catiline Champion, Ceratopus Schoenherr, Coenochira Pascoe, and Stelechodes Faust) are considered valid. It is clear, from our cursory review of the literature on this group, that a comprehensive study of the world ceratopodines is needed. Little is known about the biology or hosts for species in this subfamily, and until now, the larvae were undescribed.

The genus Ceratopus includes about 17 valid species from the neotropics (O'Brien and Wibmer, 1982; Wibmer and O'Brien, 1986). All of the larval specimens examined for this study were associated with or reared from figs (Moraceae). We examined label data for adult specimens of Ceratopus in the National Museum of Natural History, Washington, and discovered a number of individuals with host data. Ceratopus bisignatus Boheman was reared from the fruits of Ficus crassiusculus and F. glabrata. Seven or eight unidentified species were bred from one or more species of Ficus. In addition to the two species of Ficus mentioned previously, other hosts for these unidentified species were Ficus continifolia, F. radulina, and F. goldmanii.

There are few published host associations for ceratopodines, and these are all for species of Ceratopus. Most of these were summarized in Lima (1956) or Silva et al. (1968). Günther (1935) noted that Ceratopus bisignatus and C. tessellatus Champion develop in the fruits of Ficus crassiusculus; Bondar (1947) reported that C. bondari (Voss) and C. sampsoni Bondar develop in the fruits of Ficus sp.; and Hustache (1940) described a new species, C. fici, whose larva was found in the fruits of Ficus. The only recorded non-Ficus host association involves another genus of Moraceae; Hustache (1940) described a new species, C. helicostylis, whose larva was found developing in the fruits of Helicostylus poeppigiana.

The methods for examining larval specimens and preparing illustrations are those used in previous work on baridine Curculionidae (Pakaluk, in press; Pakaluk and Carlow, 1994). The nomenclature for larval structures follows Anderson (1947), but some modifications introduced by May (1967) are used. These modified terms are restricted to the prementum, because Anderson did not denote terms to differentiate between the ligular and prelabial setae. The range for body length was measured from presumed last instar larvae. All illustrations were prepared from slide-mounted specimens using a drawing tube with a Leitz Diaplan compound microscope with Nomarski differential-interference contrast illumination. All specimens examined for this study are deposited in the alcohol and slide collections of Coleoptera larvae in the Smithsonian Institution's National Museum of Natural History, Washington.

## Description of late instar larva of Ceratopus sp.

(Figs. 1-9)
Length $4.50-4.90 \mathrm{~mm}$. Body moderately slender, strongly curved, subcylindrical. Head orange. Pronotum with sclerite divided medially.

Head (Figs. 1, 2) free, length and width subequal. Anterior stemma present; posterior stemma absent. Antenna (Fig. 3) with sensory appendage conical, about $2.0 \times$ longer than longest conical rod. Epicranial suture distinct; coronal suture reaching posterior margin of cranium, slightly less than $0.5 \times$ length of head; frontal arms meeting at about $105^{\circ}$ angle. Endocarina indistinct. Frontal setae $1-5$ present, setae 4 and 5 longest, subequal in length, about $6.0 \times$ longer than seta 3 , setae $1,2,3$ short, subequal in length. Dorsal epicranial setae 1-3 longest, subequal in length, about $4.0 \times$ longer than seta 4 , seta 4 shortest, about $0.33 \times$ length of seta 5 . Lateral epicranial setae 1,2 long, seta 2 slightly longer than seta 1 . Ventral epicranial setae present, seta 1 about $3.0 \times$ longer than seta 2 . Clypeus (Fig. 5) about $3.8 \times$ wider than long, widest subbasally, clypeal seta 1 slightly longer than seta 2 , with distinct clypeal sensilla. Labrum (Fig. 5) about $3.7 \times$ wider than long, widest at base, lateral edges subparallel to weakly convergent, with anterior edge distinctly produced medially, labral seta 1 subequal in length to seta 2 , seta $26.0 \times$ longer than seta 3 , with a pair of lateral sensilla, median sensillum absent. Labral rods (Fig. 6) slightly longer than clypeus at midline, weakly convergent basally. Epipharynx (Fig. 6) with 3 pairs of anterolateral setae, 3 pairs of anteromedian setae, and 2 pairs of median setae, posterior pair smaller, shorter, slightly closer together, with a pair of sensory pores in clusters of 3, minute asperities mesally. Mandible (Fig. 9) with 2 apical teeth. Maxilla (Figs. 7, 8) with palp 2 -segmented, basal segment with 1 seta, 1 pore, apical segment with 1 pore; mala (Fig. 8) with 5 ventral setae, 7 dorsal setae. Labium (Fig. 7) with palp 2 -segmented, each with a single pore; prementum with 2 pairs of setae, sclerite as in Figure 7, anterior process broad, biemarginate apically, extending to apex of ligula, posterior process elongate, rounded apically, with 2 pairs of setae, ligular seta short, prelabial seta long, about $3.0 \times$ longer than ligular setae, with a pair of pores; postmental seta 2 longest, slightly longer than seta 1 , about $2.0 \times$ longer than seta 3.

Pronotum with 11 setae, 5 moderately long, subequal, others shorter. Spiracle bicameral, with air tube subequal in length to diameter of peritreme. Prodorsum of meso- and metathorax without setae; postdorsum of each segment with 4 setae, setae


Abdomen with 8 pairs of bicameral spiracles laterally, with air tubes subequal to slightly shorter than diameter of peritreme (Fig. 4). Dorsal fold 1 absent. Sternellum absent. Prodorsal seta present on VIII. Segments I-VII with 5 postdorsal setae, VIII with 3 setae, IX with 2 setae, abdominal segments usually with setae $1,2,4$ short, 3 and 5 long. Spiracular area with 2 setae, one seta short, the other minute. Epipleurum with 2 setae, one seta short, the other long. Pleurum with 2 setae, one seta short, the other long. Pedal and eusternal area with setae short, subequal in length. Anus terminal, with 7 lobes, bilobate dorsally, trilobate ventrally. Asperities fine, inconspicuous, generally distributed over body, slightly less dense laterally.

The description and illustrations were based upon a single, slide-mounted specimen that was with material reared to adults from San Juan, Honduras. Other larval specimens were compared to assess variation and to incorporate character data from alcohol-preserved specimens, such as for body length or color. The specimens examined (listed below) represent at least two different species of Ceratopus, although there appears to be little if any variation between them.

Material examined. Fifty-five specimens (4 slides, 51 in alcohol) were examined with the following collecting data: HONDURAS. Progresso, from fig fruit, W. M. Mann; same data except 1029, from large wild fig fruit; same data except 14 March 1920, from fig; San Juan, 23 March 1920, from large fruited fig, W. M. Mann. MEXICO. No specific locality, 6 August 1951, in seed capsule of Ficus sp., w-1496, USDA \#51-6990; Atlixco Puebla, 23 May 1937, in wild fig, A. Stone; near Tampico, October and November 1913, found abundantly attacking wild figs, D. L. Crawford. PANAMA. No specific locality, intercepted 7 April 1972 at Miami, Florida \#003970, Ficus sp. fruit, USDA \#72-6074.
A single slide is labelled "Progress. Honolulu". We interpret this as a lapsus for Progresso, Honduras, since the other label data are consistent with other specimens from this locality. Some larvae were associated with specimens ultimately reared to adults, while the remaining specimens were identified by comparing them to these reared lots.

Although the Ceratapodinae have historically been treated as a separate subfamily, Kuschel (1982, and in Wibmer and O'Brien, 1986:205) suggested that this group should be incorporated into an expanded Curculioninae (Curculionini of Kuschel's (in press) latest classification, and followed by May (1993)). The larva of Ceratopus described above differs from the curculionine diagnosis presented by May (1993) by having an indistinct endocarina and a broad, enlarged premental sclerite. Most other curculionines have a distinctly trident-shaped premental sclerite, except for leafmining forms, such as species of Geochus Broun and Neomycta Pascoe. Perrin (1992a, b) discussed the ecology of species of Curculio developing on species of Ficus and Fagales. She suggested that there were two independent radiations on host plants within this genus. These host plant data may support a close relationship between ceratopodines and Curculio and its relatives.

It is beyond the scope of this paper to elucidate the systematic placement of this subfamily based upon larval data. We intend only to make these morphological data available to others studying the immature stages of Curculionoidea, with the hope that the description and illustrations of this Ceratopus larva will eventually contribute to clarifying the relationship of ceratapodines to other weevils.

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# A REMARKABLE NEW BAMBOO LYGAEID FROM MEXICO AND A NEW SPECIES OF PATRITIUS FROM VENEZUELA (HEMIPTERA: LYGAEIDAE: BLISSINAE) 

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#### Abstract

Toonglasa indomita and Patritius osuna are described as new species from Mexico and Venezuela respectively. The former is noted to have spectacular elongate spines protruding from the posterior end of the male 8 th abdominal segment. A discussion is included of the sexual dimorphism in species of Toonglasa and the reasons for this are hypothesized. New bamboo host plants are included for previously described species of Toonglasa.


Recent years have seen the addition of many new species of bamboo living Blissinae in the Western Hemisphere. Most of these species are placed in the genus Toonglasa Distant (Slater and Brailovsky, 1983, 1990).

One of the remarkable features of species of Toonglasa is the variety of secondary sexual structures of the male abdomen. These occur in a variety of conditions often involving different segments such as a series of spinules on most of the abdominal sternites, as swellings of the posterior segments to form a rather annulate appearance, as elongations of the connexivum and adjacent area of the seventh abdominal segment to form somewhat "pincer-like" protrusions and as various small spines and ridges on the eighth abdominal sternum. The species described below has carried this last development to an extreme condition in which the ventral surface of segment eight is produced into three very elongate, serrate, needle-sharp spines that project over the genital capsule (Figs. 1, 2) and are connected at their bases by a ridge bearing a series of serrate spinules.

The development of these caudal secondary structures in a subfamily which otherwise rarely shows such conditions is difficult to explain. It is true that other Blissinae show sexual dimorphism, but usually as spines and "tusks" on the head. In the Oriental and Australian genus Pirkimerus Distant (also bamboo feeders) the bucculae of the males are often strongly and bizarrely produced (Slater and Ahmad, 1965).

The reason for this phenomenon is unknown. David Wagner (pers. comm.) has suggested that because bamboos, especially in the New World, are a limited and long lived group speciation in such situations frequently involves secondary sexual structures to reinforce species recognition and avoid mating mistakes. Such a hypothesis would imply that several species use the same species of host plant. This does appear likely to be the case in Toonglasa as more than one species has been taken breeding on a single host and several species appear to breed on more than one species of bamboo. This is in contrast to what is known of many species of such large genera


Fig. 1. Toonglasa indomita, new species. Eighth and ninth male abdominal segments dorsal view.
as Ischnodemus and Blissus which are primarily grass feeders and tend to be host specific (Slater, 1976).
Some species of Patritius also breed on bamboo. This genus was revised by Slater (1979) and we take this opportunity to describe an additional species of these rarely collected insects.

## Toonglasa indomita, new species

Relatively robust, elongate, parallel sided. Head, anterior two-thirds of pronotum, scutellum, clavus, distal one-half of corium, basal two-thirds of membrane, distal one-half of fourth antennal segment, head below, thoracic pleuron and sternum black.


Fig. 2. Toonglasa indomita, new species. Eighth and ninth male abdominal segments ventral view.

Posterior pronotal lobe, abdominal sternum (except for connexiva) and coxae dark chestnut brown. Basal two-thirds of corium and apical one-third of membrane translucent, light gray-yellow. First three antennal segments and basal one-third of fourth antennal segment yellow. Body above completely shining, polished, except for a narrow gray pruinose basal area of scutellum. Pruinose below on venter of head and prothorax between coxae. Large dull evaporative area covering entire anterior lobe of metapleuron and posterior edge of mesopleuron. Head and pronotum with scattered, elongate upstanding hairs. Vertex, anterior pronotal collar and broad central area of pronotum punctate, latter punctures irregular and anastomosing.

Head non-declivent, eyes large set on short head extensions, remote from anterolateral pronotal angles. Length head 0.64 , width 0.84 , interocular space 0.50 . Pronotum with well developed anterior collar, lateral margins broadly rounded on anterior one-half, straight sided from transverse impression to humeral angles; calli large, covering most of anterior lobe, impunctate; posterior pronotal margin concave. Length pronotum 1.29 , width 1.60 . Scutellum rugosely punctate, a distinct median carina present. Length scutellum 0.66 , width 0.70 . Length claval commissure 0.60 . Midline distance apex clavus-apex corium 1.20. Midline distance apex corium-apex abdomen 1.92. Membrane extending posteriorly midway over seventh abdominal
tergum. Apex of abdomen sinuately truncate with caudo-lateral corners of abdominal tergum seven with a downcurved sharp, semi-recurved spine. Eighth abdominal segment ventrally with three elongate slender sharp upcurved spines extending well over most of genital capsule, outer spines with sharp spinules along lateral margins (Figs. 1, 2). Metathoracic scent gland auricle elongate, strongly curved anteriorly, apex rounded. Forefemur strongly incrassate, ventrally narrowed to a sharp ridge bearing distally a single large outward curving black tipped spine. Labium short, extending well onto prosternum, but not attaining forecoxae; third segment exceeding base of head by about one half its length. Length labial segments I 0.32 , II 0.20 , III 0.18 , IV 0.22 . First antennal segment slightly exceeding apex of tylus, segments II and III slender, filiform, segment IV fusiform. Length antennal segments I 0.20 , II 0.54 , III 0.56 , IV 0.74 . Total body length 6.64 .

Holotype: Male: MEXICO: Chiapas: Reserva: El Ocote. 30.IV. 1993 (E. Barrera). In UNAM.
Paratypes: 2 males, 4 females. Same data as holotype. In UNAM and J. A. Slater Collections.

Adults and nymphs were taken breeding on the bamboo Rhipidocladum pittieri (Hack) McClure.

Toonglasa indomita will key to couplet 17 in Slater and Brailovsky (1990). Species at this couplet are separated by whether or not there is an elongate protrusion extending posteriorly from abdominal connexivum seven. $T$. indomita does not pass readily through either side of the couplet. It does not have an elongate process extending backward from the end of the connexivum, but there is not a simple end to the connexivum either. Rather the connexivum ends in a short, downward bent and recurved hooked spine at the end of the connexivum which is readily visible as the end of the abdomen is markedly truncate. T. indomita is most closely related to T. elegans Slater and Brailovsky (see fig. 1 in Slater and Brailovsky, 1990) resembling the latter in the shining dorsal surface, general coloration and pale yellow appendages. $T$. indomita is a broader more robust species, has only the base of the scutellum pruinose (scutellum entirely pruinose in elegans). T. elegans has the propleuron and mesopleuron pruinose whereas these areas are polished and shining in indomita. These pruinosity differences will separate females of the two species. Males of course are readily separable by the striking differences in the posterior segments of the abdomen. The color and texture of the hemelytra are also very different in the two species. In elegans the clavus and corium are both dull with the corium laterally pale contrasting with the suffused gray-brown central area. In indomita the hemelytra are polished and shining and the corium is pale on the proximal half and almost black distally. The metathoracic scent gland auricle of indomita is more elongate and more strongly curved anteriorly than it is in elegans. Such other dorsally non-pruinose species of Toonglasa as collaris (Signoret) and collaroides (Slater and Wilcox) agree with elegans in having the scutellum, propleuron and mesopleuron pruinose.

## ADDITIONAL RECORDS OF TOONGLASA

Toonglasa tumorosis Slater and Wilcox. 5 males, 1 female. MEXICO: Chiapas: 10 km al sur o al Sw de Jaltenango 4.V. 1993 (E. Barrera). On the bamboo Arthostilidium excelsum Griseb.

Toonglasa umbrata (Distant). 5 males, 1 female. MEXICO: Chiapas: 20 km Carrl. Tuxtla Gutierrez Ocozocoautla 30.IV. 1993 (E. Barrera).

Patritius osuna, new species
Head, anterior pronotal lobe, scutellum, corium, membrane of forewing, thoracic pleura and sterna black. Posterior pronotal lobe, clavus, explanate corial margins and abdominal sternum dark reddish brown, latter becoming lighter laterally and caudally. Legs uniformly pale yellow. Antennae light brown, tinged with yellowish, distal third of fourth segment black. Body surface almost completely strongly shining contrasting strongly with dull surface of forewing membrane and a narrow dull strip along outer margin of clavus and adjacent area of corium. Dorsal surface appearing nearly glabrous but a few short upright hairs present on all dorsal surfaces.

Head non-declivent; tylus reaching middle of first antennal segment. Eyes set on short lateral head projections and well away from anterior margin of pronotum. Length head 0.80 , width 1.02 , interocular space 0.74 . Pronotum with distinct anterior collar delimited posteriorly by a series of coarse punctures; lateral margins sinuate, tapering from humeral angles to anterior margin; transverse impression shallow and incomplete mesally; calli impunctate, slightly impressed. Posterior pronotal lobe with small scattered inconspicuous punctures, posterior margin deeply concave. Length pronotum 1.80 , width 2.36 . Scutellum coarsely punctate with prominent median carina. Length scutellum 1.0, width 1.20. Lateral corial margins straight; membrane extending midway over seventh abdominal tergum. Length claval commissure 0.76. Midline distance apex clavus-apex corium 1.60. Midline distance apex corium-apex abdomen 3.44. Metathoracic scent gland auricle crescent shaped, strongly curving anteriorly with blunt apex. Fore femur strongly incrassate, armed below on distal third with one large curved spine and 4 smaller spines, 2 on inner surface and 2 on outer, both series distad of large spine. Middle and hind femora moderately incrassate, armed distally with 2 or 3 small blunt spines. Labium exceeding forecoxae, reaching mesosternum, but remote from mesocoxae. Length labial segments I 0.48 , II 0.54 , III 0.50 , IV 0.34 . Antennae slender, filiform, fourth segment narrowly fusiform. Length antennal segments I 0.32 , II 0.96 , III 0.78 , IV 1.0. Total body length 9.88 . Holotype: Female: VENEZUELA: Chiragua. Carabobo. 1,700 m. 17.VII. 1968 (J. \& B. Bechyne). In Universidad Central, Maracay, Venezuela.

This species will key to P. fuscovenosus Stål in Slater (1979). It is however not closely related to any of the species in this section of the key, all of which have extensive areas of pruinosity on the dorsal surface. However, the anteriorly curving scent gland auricle directs osuna to this section of the key. It actually is much more similar in habitus to $P$. englemani and $P$. columbianus both of which have completely shining dark pronota, but both have posteriorly curving scent gland auricles. In addition columbianus has a pruinose scutellum, englemani has strongly stalked eyes, is heavily spinose on all femora, has a third labial segment longer than either segments two or four and a bright yellow clavus and corium.

It is a pleasure to dedicate this new species to Dr. Eduardo Osuna for his contributions to our knowledge of Venezuelan Hemiptera.

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# A DESCRIPTION OF THE IMMATURE STAGES OF PADUNIELLA NEARCTICA (TRICHOPTERA: PSYCHOMYIIDAE) WITH NOTES ON ITS BIOLOGY 

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#### Abstract

Larva and pupa of the genus Paduniella are described for the first time based on specimens of Paduniella nearctica Flint from the Ozark Mountains of Missouri and Arkansas, U.S.A. Larvae of Paduniella differ from Tinodes and Lype in having well developed teeth along the concave margin of the anal claw; they can be distinguished from larvae of Psychomyia by the submental sclerites being wider than long and small rather than longer than wide and large. The pupa of Paduniella is unique among Nearctic psychomyiids in having 6 -segmented maxillary palpi, 4 -segmented labial palpi, and 3 pairs of labral setae. Observations on the biology of the species suggest a scraper functional role for the larva and a bivoltine life cycle.


Adults of the genus Paduniella are unusual among the Trichoptera in having 6 -segmented maxillary palpi and 4 -segmented labial palpi. First erected by Ulmer (1913), the genus currently includes 25 species. Twenty-four of these are distributed in the Palaearctic, Oriental, and Afrotropical biogeographical regions. Only one species, P. nearctica Flint, is known from the Nearctic region where it is restricted to the Ozark Mountains of Arkansas and Missouri, U.S.A. (Flint, 1967; Bowles and Mathis, 1989; Mathis and Bowles, 1992). Current knowledge of the genus is limited to morphology of adult males and females of a few species. Nothing is known with regard to immature stages or their biology. Herein we describe the larva and pupa for the genus based on specimens of $P$. nearctica and offer some observations on the biology of this species. Setal nomenclature follows that of Williams and Wiggins (1981).

## Paduniella nearctica Flint, 1967

Paduniella nearctica Flint, 1967, p. 311, figs. 1-4.
Larva (Figs. 1-5). Length of heat-killed, straightened larvae $5.7-7.2 \mathrm{~mm}, \bar{x} 6.4 \mathrm{~mm}$ $(\mathrm{N}=17)$; head capsule width $0.46-0.58 \mathrm{~mm}, \bar{x} 0.52 \mathrm{~mm}(\mathrm{~N}=191)$. Sclerites of head and pronotum light brown, without conspicuous patterns; mesothorax, metathorax, and abdomen white, yellow, or green with broad dark line running longitudinally along dorsum. Head capsule (Figs. 1-3) with 18 pairs of tactile setae, 5 pairs of proprioceptic setae, and 1 unpaired and 17 paired pit setae; pit seta 11 (P11) absent; antennae lacking prominent sensilla, each with 3 short, stout setae. Ventral apotome small, V-shaped, arms extended. Labrum fully sclerotized, with 6 pairs of tactile setae and 1 unpaired and 2 pairs of setal pits. Mandibles (Fig. 5) slender, each bearing 2 setae near midlength on lateral surface; left mandible with 2 large teeth dorsally


Figs. 1-5. Paduniella nearctica, terminal instar larvae. 1. Larva, lateral view. 2. Head, ventral view. 3. Head and thorax, dorsal view. 4. Larval tube. 5. Mandibles, dorsal view.
and numerous smaller teeth along ventral cutting edge; right mandible with prominent tooth apically, distinct notch located near midlength of mesal face. Maxillae each lacking well defined cardo and stipes, bearing single prominent seta laterally; palpifer present, bearing 1 seta; palpi 4 -segmented, third segment longest; galea rounded, bearing numerous small hair-like setae, 2-4 tactile setae, and 4 or 5 sensilla. Labium bulbous basally, forming long narrow tube anteriorly that extends beyond the head, palpi absent; submental sclerites small, triangular, bearing 1 seta each.
Pronotum (Fig. 3) sclerotized, each half with 12-17 tactile setae, 3 pit setae, and 3 proprioceptic setae; anteromesal proprioceptor (seta 13) absent. Prosternum with 4 pairs of proprioceptic setae. Propleuron bearing two tactile setae; trochantin broad, flat, with 2 proprioceptic setae. Meso- and metanota each with 6 pairs of tactile setae ( 1 at sal, 3 at sa2, and 2 at sa3), 1 pair of setal pits, and 3 pairs of proprioceptic setae. Meso- and metasterna each with 3 pairs of proprioceptic setae. Meso- and metapleura each a narrow sclerotized band; with two tactile setae and 2 proprioceptors in adjacent areas. Thoracic legs with primary setae only; prothoracic legs longer and stouter than those of other segments, bearing dense brush along mesal margin of tarsus; tarsal claws of all legs bearing 2 stout setae.
Abdomen dorsoventrally flattened, gills and lateral fringe absent; 5 anal papillae present, palmately arranged when extended; abdominal segment I distinctly shorter than other anterior segments. Segments I-VIII each bearing 5 pairs of tactile setae dorsally, 2 pairs laterally, and 3 pairs ventrally; segment IX lacking lateral setae; 2 pairs of dorsal and 1 pair of ventral proprioceptors present on most segments (segment I lacking ventral proprioceptor, segment IX lacking dorsal proprioceptors); setal pit 2 (P2) absent on all segments. Basal segment of each anal proleg bulbous, shorter than distal segment, bearing single small seta; lateral sclerite with 8 tactile setae, one seta on lateral surface, group of 6 long setae at posterior end, and smaller seta just anterior to this basal tuft. Anal claw with 4 stout teeth along ventral concave margin, fourth tooth one-half length of more anterior three; with 9 tactile setae and 2 prominent setal pits.

Larval tube (Fig. 4) constructed of sand grains and debris in depressions on surfaces of larger rocks; expanded slightly at ends; up to 22 mm in length and 2 to 3 mm wide.
Pupa (Figs. 6-10). Length $3.1-4.4 \mathrm{~mm}(\mathrm{~N}=10)$. Head (Fig. 6) with 2 pairs of setae on frons; antennae each 24 -segmented, scape with 3 short setae, other segments glabrous. Maxillary palpi each 6 -segmented; labial palpi 4 -segmented. Labrum (Fig. 8) with 3 pairs of setae located in 2 groups at anterolateral corners, setae without hooked apices. Genae each with two groups of 3 setae located near articulation points with mandibles. Mandibles (Fig. 9) long, slender; each tapering to short, narrow filament bearing 4 hooks near apex; with 2 setae near base and distinctly serrate cutting edge. Abdomen (Fig. 7) lacking gills and lateral fringe; base color white with black coloration dorsally, most intense near midline; abdominal hook plates with 410 well-developed hooks, located anteriorly on segments II-VIII and posteriorly on segment V ; segment V with a dense bed of posteriorly directed spines just anterior to posterior hook plate. Anal processes (Figs. 7, 10) long; each divided into a small rounded, mesal lobe and long tubular lateral lobe; lateral lobe with a row of anteriorly directed spinules on venter and 8 apical setae with hooked apices. Pupal case constructed of sand grains and debris; smaller than larval tube, $7-9 \mathrm{~mm} \times 3-3.5 \mathrm{~mm}$; capped on both ends by a silken sieve plate.


Figs. 6-10. Paduniella nearctica, pupa. 6. Head, facial view. 7. Abdomen with sclerotized hook plates enlarged, dorsal view. 8. Labrum, dorsal view. 9. Mandible, dorsal view. 10. Anal process, lateral view.

Specimens examined. Arkansas, Washington County, Cove Creek, 12 mi south of Prairie Grove, 16 Apr. 1989, 2 larvae, Mathis; as above, 30 May 1989, 2 larvae; as above, 25 June 1989, 1 larva, 1 pupa; as above, 23 July 1989, 12 larvae; as above, 30 July, 29 larvae; as above, 5 Aug. 1989, 22 larvae; as above, 12 Aug. 1989, 20 larvae, 7 pupae; as above, 20 Aug. 1989, 31 larvae, 32 pupae; as above, 16 Sept. 1989, 20 larvae; as above, 25 Oct. 1989, 9 larvae; as above, 3 Jan. 1990, 57 larvae. Stone County, North Sylamore Creek, at Barkshed Recreation Area, 12 Mar. 1991, 6 larvae, Moulton and Abbott.
Diagnosis. The larva of Paduniella nearctica exhibits characteristics consistent with those of other members of the family Psychomyiidae; the prothoracic trochantin is broad and flat, the labium is extended beyond the anterior margin of the head, labial palpi are absent, and the prothoracic legs are stouter than those of other segments. Larvae of $P$. nearctica can be distinguished from those of other Nearctic psychomyiid genera based on two characteristics. The well-developed teeth on the concave margin of the anal claw distinguish Paduniella from larvae of Tinodes and Lype in which teeth are lacking (Wiggins, 1977). The submental sclerites of $P$. nearctica differ from those of Psychomyia being small and wider than long rather than large and longer than wide (Wiggins, 1977). The pupa of $P$. nearctica has 6 -segmented maxillary and 4 -segmented labial palpi which allows for easy separation from all other psychomyiids. The pupa is unique also in having only 3 pairs of labral setae rather than 5 pairs as is reported for pupae of the other Nearctic genera (Lepneva, 1964).
Habitat and biology. During the course of surveys for Trichoptera of the Interior Highlands, we have collected adults of $P$. nearctica from a number of headwater streams throughout the Ozarks of Arkansas and Missouri (Bowles and Mathis, 1989; Mathis and Bowles, 1992). These streams are among the least impacted in the region suggesting that the species may be intolerant to anthropogenic pollution and disturbances. At the type locality where we collected most of the specimens for the present investigation, the larvae of $P$. nearctica inhabited areas with low velocities and large stable substrates. Their tubes were constructed on the upper surfaces and sides of rocks typically within cracks and depressions. Analysis of gut contents revealed that larvae fed almost exclusively on diatoms during the winter ( $88 \%$ of food based on particle size), but, during the summer, detritus also was important ( $73 \%$ diatoms and $17 \%$ detritus). These food habits suggest a scraper functional role for the species (Merritt and Cummins, 1984). The shape of the larval mandibles having a welldeveloped cutting edge also suggests a scraper functional role for $P$. nearctica.

Although exhaustive sampling was not performed, some observations of the life history of $P$. nearctica were collected. Larvae overwintered as terminal instars, initiating pupation during late May to early June. A second period of pupation occurred in early to mid August suggesting that the species may be bivoltine. Adults have been collected from mid May until mid September (Bowles and Allen, 1988; Bowles and Mathis, 1989; Mathis and Bowles, 1992), but peak abundances occur at times corresponding to these periods of pupation. The biology and life history of the species were the subject of a recent investigation from which results should be available shortly (S. Williams, pers. comm., 1993).

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# A NEW SPECIES OF LEOTICHIUS FROM BALI, WITH NOTES ON IMMATURE STAGES AND HABITAT (HETEROPTERA, LEPTOPODIDAE) 

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#### Abstract

Leotichius shiva new species is described from the Kehen Temple at Bangli, Bali and compared with the two previously described species of Leotichius. The Bali habitat, shared with numerous ant lion larvae, consisted of very dry unconsolidated earth sheltered by the multiple roofs of the Hindu shrines. Nymphs of several instars are discussed and compared to other Leptopodomorpha.


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In 1983 Ernst Heiss presented JTP with two Leotichius specimens that he had collected at the Kehen Temple at Bangli, Bali. During their National Geographic Society Expedition to the Malay Archipelago, J. T. and D. A. Polhemus visited this site and collected a good series of these insects, including the first known immatures. Not surprisingly these represent a new species which is described below.

The genus Leotichius was established by Distant (1904) for his new species L. glaucopis from Burma, and placed in the family Saldidae, subfamily Leptopinae (=Leptopodidae). The family Leotichiidae was erected by China (1933) to hold Distant's species, and later he (China, 1941) described a second species L. speluncarum from limestone caves at Gua Berang, Perlis Province, Peninsular Malaysia. Schuh and Polhemus (1980) placed Leotichius in the family Leptopodidae, subfamily Leptopodinae, a placement followed by Schuh, Galil and Polhemus (1987) in a world catalog of Leptopodomorpha. Habitat data were lacking for glaucopis, but because speluncarum was found running on bat guano deposits in shallow caves, and no more specimens were collected during the more than forty intervening years between that collection and the present, it became accepted that Leotichius were cavernicolous. The discovery of these insects on Bali suggests that their preferred habitat is fine dry soil sheltered from rain, and in Bali at least shared by the larvae of xeric adapted Neuroptera. Their occurrence in cave mouths would thus be expected due to the sheltered nature of that habitat.

One specimen of Leotichius, species unnamed, is known from Thailand, but there is no habitat data (Pericart and Polhemus, 1990).

Leotichius shiva, new species
Figs. 2, 4-12
Diagnosis. Leotichius shiva is closely related to L. glaucopis and speluncarum. It differs from speluncarum by the more lateral position of the tubercles on the posterior


Figs. 1-3. Pronota of Leotichius spp. 1. L. glaucopis. 2. L. shiva. 3. L. speluncarum.
margin of the pronotum, different dark banding on the legs, more strongly raised scutellar apex, and from both species by the spatulate spines ventrally on the fore and middle femora. L. glaucopis differs from both of the other species by the longer first and second antennal segments, more sharply angled and more posteriorly located humeral pronotal angles, and other characters as noted by China (1941).

We have studied the holotype of Leotichius glaucopis Distant and a paratype of


Fig. 4. Hind wing, L. shiva.


Figs. 5-8. Scanning micrographs, L. shiva. 5. Dorso-frontal view of left side of head, fifth instar nymph. 6. Antennal segments 3 and 4. 7. Lateroventral view of pretarsus, early instar nymph. 8. Lateroventral view of tarsus, adult.

Leotichius speluncarum China in order to construct Table 1 that illustrates differences between the known species. Both of these specimens, located in the British Museum (Natural History), are in rather poor condition.
Description. Macropterous male (all measurements in mm): Ground color yellowish brown, head above eyes, most of scutellum, three broad fasciae along costal margin (basal, medial, distal), fuscous to piceous; broad areas on pronotum and hemelytra variably infuscated; membrane weakly infuscated basally and medially. Legs leucine to testaceous, each femur with a subapical brown annulus with width equal to diameter of femur; femora and tibiae distally dark. Venter of abdomen, head and anterior part of pronotum, coxae, brown. Venter of head and prothorax, all ventral thoracic sutures and margins with a thick build up of cotton-like substance (Figs. 9, 10).

Structural characteristics: Base of head, prothorax except ventral area behind head, hemelytra except membrane, acetabulae, densely, regularly punctate (areolate). Head short, more than twice as wide as long in middle; frons, ventral area between hind margin of eyes and thorax set with thickened blunt setae; eyes very large, strongly exserted; non-functional dorsally, with tubular setae (Fig. 5); ocelli prominent, set on strongly raised tubercle. Antennae moderately long, segments 1 and 2 stout,


Figs. 9-12. Scanning micrographs, L. shiva. 9. Lateral view of meso- and metathorax. 10. Detail of cottony substance shown in Figure 9. 11. Lateroventral view of female terminal abdominal segments, including ovipositor. 12. Detail of clubbed setae in Figure 11.
segments 3 and 4 slender (Fig. 6); segment 1 with 2 long stout setae; segments 1 and 2 with numerous short, thickened setae (Fig. 6); length of segments I-IV: 0.43, 0.36, $0.29,0.43$. Pronotum short, broad, strongly narrowed anteriorly, with a prominent longitudinal median carina; four tubercles $(2+2)$ of calli prominent, strongly raised posterior margin rounded, with two $(1+1)$ small tubercles adjacent to anterior angles of scutellum (Fig. 2); length on midline, 0.60 . Hind wing with reduced venation (Fig. 4). Legs relatively slender, hind tibia distinctly sinuate. Forefemur slightly incrassate, armed beneath with two irregular rows of four or five stout spatulate setae, those of each row divergent; fore tibia armed beneath with a double row of divergent longer bristles. Middle femur armed beneath with a row of erect spines of varying lengths, and a second parallel row of very short spines; middle tibia armed beneath as fore tibia, dorsally with longer sub-erect spines. Hind legs only with short fine setae. Pertarsus with accessory parempodia and reduced parempodia (Fig. 8).

Proportions of legs as follows: Femur, Tibia, Tarsal 1, Tarsal 2: Anterior, 0.56, $0.50,0.20$, -; Middle, $0.70,0.55,0.13,0.18$; Posterior, $0.93,1.15,0.35,0.25$.

Table 1. Comparison of Leotichius species.

| Character | shiva | glaucopis | speluncarum |
| :---: | :---: | :---: | :---: |
| Antennal ratio | 10:8:14:12 | 10:8:16:12 | 12:10:17:13 |
| Pronotum shape (lateral view) | tumid posteriorly | tumid posteriorly | not tumid posteriorly |
| Posterior pronotal tubercles | obsolete; located at anterolateral angles of scutellum | small; located mesad of anterolateral angles of scutellum | pronounced; located at anterolateral angles of scutellum |
| Pronotal longitudinal carina | pronounced | pronounced; keel-like | weak posteriorly |
| Lateral margins of scutellum | moderately raised | strongly raised; carinate | moderately raised |
| Scutellar apex | weakly compressed; weakly raised | strongly compressed; strongly raised | weakly compressed; not raised |
| Leg coloration (dark banding) | narrow subapical annulation | narrow subapical annulation | broad subapical annulation |
| Costal margin of hemelytra at membrane | continuous | continuous | disjunct |
| Venation of fore wing membrane | 3 closed cells | 3 veins | 2 veins |

Male genitalia as shown by China (1941:fig. 2) for L. speluncarum.
Length, 2.18 mm ; width across pronotum 0.95 mm .
Macropterous female: Structure and coloration mostly as in male. Length, 2.33 mm ; width, 1.05 mm . Ovipositor externally as in Fig. 11.
Description of immatures: A number of females were dissected in an effort to obtain ripe ovarian eggs, without success. Only one poorly formed egg was found, suggesting that these insects may have a distinct breeding season restricted to the rainy season with higher humidity.

Eyes: In a third instar nymph, the earliest available, the dorsal flattening of the eyes is already apparent, and is accentuated in later instars. The ommatidia are not formed dorsally, but instead the long basal part of the laterally directed ommatidia are visible, lying parallel to the dorsal surface just beneath a thickened but still transparent dorsal cuticular covering (Fig. 5).

Antennae, legs: The nymphal antennae and legs are similar to the adults in shape and complement of setae and spines. The single segmented tarsi are without visible pretarsal structures, except two long claws (Fig. 7).

Abdomen: Spiracles are present ventrally on the laterotergites of abdominal segments $2-8$; the first abdominal spiracle lies along the hind coxae. On sternum 2 just caudo-medially from the first abdominal spiracle, a small opening underlain by bright pink tissue suggests the presence of an active gland, possibly homologous with the larval organ of Saldidae (see Cobben, 1957; Polhemus, 1985).

The posterior margin of each abdominal tergum is set with a row of spines. A single abdominal scent gland is located on the anterior margin of tergum four, with
a small obscure opening, not underlain by orange or pink glandular tissue, indicating that this gland may be non-functional.
Material examined. Holotype, male: INDONESIA, Bali Prov., Bali, Bangli, Kehen Temple, October 17, 1985, CL 2169, J. T. and D. A. Polhemus (AMNH).

Paratypes: INDONESIA, Bali: many males, females, same data as holotype (JTPC, AMNH, USNM, MZB, BMNH); 1 male, 1 female, same locality as holotype, July 28, 1980, Ernst Heiss (JTPC).
Additional specimens: Numerous nymphs, same data as holotype (AMNH, JTPC, USNM).
Etymology. The name shiva, a noun in apposition, refers to the Hindu god Shiva, creator and destroyer of worlds.
Habitat data. The type locality at Bangli consists of Hindu temples set on a raised terrace against a sloping forested hillside. The largest shrine is that of Shiva with 11 roofs, one over the other, sheltering a raised platform having a surface of unconsolidated desiccated earth; other adjoining temples of lesser gods are of the same design but with fewer roofs. The desiccated earth of these temples, pocked with conical ant lion pits, was the only place that Leotichius was seen, although dry but unsheltered earth in the vicinity was searched. This microhabitat and the only other one previously documented for these bugs (on bat guano in a limestone cave) suggests that a completely dry sheltered environment is a habitat requirement.
Discussion: The hind wing venation (Fig. 4) is quite reduced, but not as drastically as depicted by China (1933, fig. 2b) for Leotichius glaucopis. Following the latest interpretation of heteropteran wings by Wootton and Betts (1986), the primary venation in the medial region seems to be $R+M$ bifurcated distally. This venation is similar to that of Valleriola, but in the latter $\mathrm{R}+\mathrm{M}$ is shifted somewhat anteriorly. In Erianotus lanosus (Dufour), illustrated by Pericart and Polhemus (1990), R + M is shifted anteriorly almost to the wing margin, and probably misinterpreted, as Cu should probably be labelled $M$ (the reduced venation of Leptopodidae is difficult to homologize). The venation of all of these is strikingly different than that of Saldidae (see: Davis, 1961:fig. 17; Polhemus, 1985:fig. 16E). In all Leptopodomorpha studied so far $M$ and $R$ diverge distally, whereas in all Nepomorpha studied, $M$ and $R$ converge and fuse distally [Potamocoris robustus La Rivers, Ochterus barberi Viets Schell (J. T. Polhemus, unpubl.); Curicta carinata Kuitert (Keffer, 1991:fig. 16); Lethocerus americanus (Leidy), Notonecta undulata Say (Davis, 1961:figs. 18, 20)]. This suggests that synapomorphies may be found in patterns of hind wing venation.

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the U. S. National Museum of Natural History, Washington (USNM), British Museum (Natural History) (BMNH), Museum Zoologicum Bogoriense, Bogor (MZB), and the J. T. Polhemus collection (JTPC).

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# TWO NEW SPECIES OF ATRACTOTOMUS FROM SOUTHERN MEXICO (HETEROPTERA: MIRIDAE: PHYLINAE) 

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#### Abstract

Two new species, Atractotomus bicolor and A. teopisca, are described from the state of Chiapas in southern Mexico. The male genitalic structures of both species are illustrated, and scanning electron micrographs are provided for the dorsal vestiture, femoral spines and pretarsus of $A$. teopisca. The relationship of these species to other New World members of the genus is discussed.


The genus Atractotomus contains 37 species distributed in the Holarctic region from Scandinavia to the Mediterranean, and east to Korea in the Palearctic ( 6 spp .), and from central Canada to southern Mexico in the Nearctic (31 spp. - see Stonedahl, 1990). Two additional undescribed species of this genus were recently discovered in the holdings of the Canadian National Collection, Ottawa and are here described and compared to other Nearctic species. This brings the total number of species known from Mexico to 21.

## Atractotomus teopisca, new species

Figs. 1-6
Diagnosis. This species keys to A. oaxaca Stonedahl in Stonedahl (1990), but is distinguished by the narrower scalelike setae (Fig. 1; cf. Stonedahl, 1990:67, fig. 69), restricted on the dorsum to the scutellum and hemelytra, and very sparsely distributed on the lateral and ventral aspects of the body; the anterior half of the pronotum paler than the posterior half; the corium and clavus bordering claval suture, and margins of cuneus narrowly pale; and especially by the elongate posterior process of the left paramere (Fig. 6) and gonopore sclerite of vesica without spines (Fig. 5).
Description. Male. Length from apex of tylus to cuneal fracture 2.19-2.39. Dorsal aspect: Dark brown general coloration with limited yellowish brown markings; vestiture with dark, suberect, simple setae and recumbent, silvery white, scalelike setae (Fig. 1), the latter restricted to the scutellum and hemelytra, and most densely distributed either side of the claval suture and on the paracuneus. Head: Pale ventrally; tylus, jugum and lorum anterior to antennal fossae shiny fuscous; darker specimens with frons and vertex uniformly brown to dark brown; paler specimens with frons mostly yellowish brown and vertex dark brown; width across eyes $0.76-0.81$; width of vertex $0.34-0.36$; ratio of vertex width to head width $0.42: 1-0.47: 1$; head weakly produced anterior to antennal fossae, tylus not or only just visible in dorsal view; posterior margin straight, angulate; vertex weakly depressed medially; eyes occupying


Figs. 1-4. Scanning electron micrographs of Atractotomus teopisca. 1. Scalelike setae on hemelytra. 2. Dorsodistal surface of metafemur. 3. Pretarsus, posterior view. 4. Pretarsus, lateral view.
most of head height in lateral view; antennae dark brown, basal half of segment II sometimes lighter brown, inserted slightly above level of ventral margin of eye; antennal segment II linear, length 0.84-0.93; ratio of length of antennal segment II to width of head across eyes 1.09:1-1.18:1; genae narrow; gula obsolete; labium reaching to apex of mesosternum or slightly beyond. Thorax: Posterior width of pronotum 1.05-1.11; pronotum distinctly bicolored in paler specimens, with anterior half pale brownish yellow and distal half dark brown to fuscous, sometimes also with posterior angles broadly pale; anterior half of pronotum dark yellowish brown or brown in darker specimens, but always slightly paler than posterior half; propleuron pale brownish yellow, infuscated dorsally in darker specimens, sometimes with only


Figs. 5-8. Male genitalia. Figs. 5, 6. A. teopisca. 5. Vesica. 6. Left paramere. Figs. 7, 8. A. bicolor. 7. Vesica. 8. Left paramere.
apex narrowly pale; prosternum pale; mesosternum mostly fuscous; scutellum uniformly dark brown to fuscous, sometimes yellowish brown in pale specimens; peritremal disc of metathoracic scent efferent system dirty white. Hemelytra: Dark brown to fuscous with corium and clavus bordering claval suture, posterior margin of corium bordering cuneal fracture, anterior and inner margins of cuneus, and sometimes outer margin of cuneus narrowly pale; sometimes more broadly pale bordering claval suture and on margins of cuneus, and with outer margin of corium, sometimes inward to radial vein, pale brownish yellow. Legs: Coxae pale brownish yellow; femora brownish yellow with faint brown or reddish brown blotches, especially dorsally; hind femora usually more extensively darkened, especially distally, and with dark blotches more strongly developed; tibiae yellowish brown, hind pair darker distally; tibial
spines black, points of insertion on tibiae narrowly ringed with fuscous; tarsi brown or dark yellowish brown; pretarsus fuscous. Genitalia: Left paramere with long, narrow anterior process (Fig. 6); gonopore sclerite of vesica without spines (Fig. 5). Female. Length from apex of tylus to cuneal fracture 2.15-2.37; similar to male in color and structure, except second antennal segment narrower and sometimes yellowish brown on basal half to two-thirds, scutellum sometimes yellowish brown, hemelytra tending to be more extensively pale, and hemelytral membrane shorter. Etymology. Named for the type locality in Chiapas, Mexico. Distribution. Chiapas, Mexico.
Discussion. Although A. teopisca keys to A. oaxaca in Stonedahl (1990), this species is more closely related to $A$. prosopidis (Knight) based on a reanalysis of character information presented in Stonedahl (1990: see tables 1 and 2). The reanalysis was executed on Hennig86 (using m* and bb* options, and the same character additivities and outgroup taxa) as follows: (1) the two new species were added to the character matrix (characters 0 to 26) with codings $A$. teopisca $=010101000111100000-0100$ ---1 and A. bicolor $=010101000111100000101010001$; (2) in the original analysis character 26 (development of the gonopore wall with 3 character states ( 0 ) thick, heavily sclerotized; (1) thinner, moderately sclerotized; and (2) very thin, weakly sclerotized) was incorrectly coded and was changed in the reanalysis to A. acaciae (0), A. nicholi (0), A. oaxaca (0), A. prosopidis (1), and A. russatus (0). This procedure resulted in 304 equally parsimonious cladograms each with length of 112 , consistency index of 0.29 , and retention index of 0.75 . The strict consensus cladogram of the 304 cladograms maintained the magnicornis and miniatus species groups as well as node 56 of figure 185 of Stonedahl (1990); the remaining species were unresolved at node 71 . We attempted to increase the resolution of the analysis by reducing some of the missing data in table 2 as follows: character 7 for $A$. mitla (state 1 ) and $A$. nicholi (1); character 13 for A. prosopidis (1); characters 14-17 for A. albidocoxis (0000) and A. schwartzi (0000); and character 18 for A. atricolor (0), A. chiapas (1), A. rubidus (0), and A. teopisca (1). Species with missing data for characters 5-7 and $23-25$ were not recoded. The results yielded two cladograms (length 112, ci $=29$, and ri $=76$ ) with the identical topology as reported in Stonedahl (1990) and with the two new species, $A$. bicolor and $A$. teopisca, taken together as sister taxa to $A$. prosopidis and all three species forming the sister clade to the miniatus species group. Only the highly homoplasious character, labial length (character 12 , $\mathrm{ci}=14$, $\mathrm{ri}=$ 40), supports the clade containing $A$. prosopidis and the two new species. Weakly converging surface ridges of the scalelike setae (character 6) and the length of antennal segment II greater than the width of the head across the eyes in males (character 13) support the close relationship of $A$. bicolor and $A$. teopisca. Further characters indicating a relationship between $A$. teopisca, A. bicolor, and $A$. prosopidis are as follows: antennal fossa located slightly above level of ventral margin of eye (character 10); posterior margin of head angulate (character 11); antennal segment II pale at least on basal half (character 18) [The color of the second antennal segment is variable in A. teopisca, tending to be dark more often than pale, but is consistently pale in the related species $A$. bicolor]; wall of secondary gonopore of male vesica thin (character 26); and except for $A$. teopisca, spines on gonopore sclerite fine (character 24).

Holotype. Male. MEXICO, Chiapas, Teopisca, 31.VII.69, L. A. Kelton, CNC Type No. 21923 (CNC).
Paratypes. MEXICO: Chiapas: 8 males, 10 females, same data as holotype (CNC);

12 males, 8 females, Comitan, 20.VII.69, ex Acacia, L. A. Kelton (AMNH, CNC, NHM); 7 males, 3 females, 14 mi W Comitan, 15.VII.69, L. A. Kelton (CNC); 2 females, 14 km NW Comitan, $5,500 \mathrm{ft}$, 15.VIII.67, H. R. Burke \& J. Hafernik (TA\&M); 2 females, Puerto Arista, 4.VIII.69, L. A. Kelton (CNC).

## Atractotomus bicolor, new species

Figs. 7-9
Diagnosis. This species is very similar to $A$. teopisca, but is readily distinguished by the smaller average size; lorum and jugum uniformly pale; second antennal segment pale basally, with distal fourth to third fuscous (Fig. 9); and by the structure of the male genitalia, especially the shorter anterior process of the left paramere (Fig. 8) and the vesica with longer, spinose gonopore sclerite (Fig. 7).
Description. Male. Length from apex of tylus to cuneal fracture 1.93-2.33. Dorsal aspect: General coloration and vestiture as described for A. teopisca. Head: Structure as described for A. teopisca; pale brownish yellow, slightly darker dorsally; vertex often infuscated; tylus shiny fuscous; width across eyes $0.72-0.82$; width of vertex $0.29-0.34$; ratio of vertex width to head width $0.38: 1-0.44: 1$; antennal segment I shiny fuscous, narrowly pale at base and apex; segment II yellowish brown, apical fourth to third fuscous, length $0.69-0.89$; ratio of length of antennal segment II to width of head across eyes $0.93: 1-1.13: 1$; segments III and IV brown or dark brown; labium reaching to apex of mesosternum. Thorax: Posterior width of pronotum $0.88-$ 1.08; pronotum always distinctly bicolored, anterior half pale brownish yellow, distal half dark brown to fuscous; propleuron mostly pale, dorsal margin infuscated, especially posteriorly; scutellum brown to dark brown, sometimes yellowish brown anteriorly in pale specimens. Hemelytra: Color pattern as described for A. teopisca, except usually broadly pale bordering claval suture. Legs: Color as described for $A$. teopisca. Genitalia: Similar to A. teopisca except left paramere with shorter anterior process (Fig. 8) and vesica with longer, spinose gonopore sclerite (Fig. 7).
Female. Length from apex of tylus to cuneal fracture 1.90-2.17; similar to male in color and structure, except sometimes more broadly pale dorsally especially on pronotum, scutellum, cuneus and along outer margin of corium; second antennal segment narrower; and hemelytral membrane shorter.
Etymology. Named for the distinctly bicolored pronotum.
Distribution. Chiapas, Mexico.
Discussion. This species keys to couplet 16 (A. pallidus and A. prosopidis) in Stonedahl (1990), based primarily on the mostly pale second antennal segment, but is easily separated from these species by the darker general coloration, with bicolored pronotum, and especially by the long, thin posterior process of the left paramere (Fig. 8).

The relationship of $A$. bicolor and A. teopisca to A. prosopidis is further supported by the occurrence of the two species on Acacia. A. prosopidis is found on the woody legume Prosopis throughout the American Southwest.
Holotype. Male. MEXICO, Chiapas, Puerto Arista, 4.VIII.69, L. A. Kelton, CNC Type No. 21924 (CNC).
Paratypes. MEXICO: Chiapas: 21 males, 7 females, same data as holotype (AMNH, CNC, NHM); 9 males, 15 females, Comitan, 20.VII.69, ex Acacia, L. A. Kelton (CNC); 5 males, 3 females, 31 mi SE Comitan, 18.VI.65, at light, Burke, Meyer \&


Fig. 9. Atractotomus bicolor, dorsal habitus, male.

Schaffner (TA\&M); 4 males, 3 females, 28 mi W Cintalapa, 25.VI.65, H. R. Burke, J. R. Meyer \& J. C. Schaffner (TA\&M).

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Museum, London (NHM). G. J. duHeaume, International Institute of Entomology, London prepared the habitus illustration of $A$. bicolor, and I. Boler, International Institute of Entomology, London assisted with the preparation of the scanning electron micrographs.

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# NEOTYPE DESIGNATION FOR RANATRA AMERICANA EDENTULA MONTANDON (HETEROPTERA: NEPIDAE) 

Ranatra fusca Palisot de Beauvois

Ranatra fusca Palisot de Beauvois, 1820; Insectes recueillis en Afrique et en Amérique, . . . p. 235.
Ranatra americana Montandon, 1910, Bull. Soc. Roum. Sci. 19:65. (Synonymized by Hungerford, 1922, Kansas Univ. Sci. Bull. 14:436.)
Ranatra americana var. edentula Montandon, 1910, Bull. Soc. Roum. Sci. 19:66. (Synonymized by Sites and Polhemus, 1994. Ann. Ent. Soc. Am. 87:33.)
Ranatra fusca var. edentula: Hungerford, 1922, Kansas Univ. Sci. Bull. 14:447.
The variety edentula was proposed by Montandon (1910, as americana edentula) for those populations lacking the preapical tooth on the fore femur, said to occur in Pennsylvania and Texas. The two female specimens of this variety were said by Montandon (loc. cit.) to be in his collection. Because varieties were not recognized as having species group standing in those early times (now changed, see below), it is doubtful if Montandon would have labelled these specimens as types. The data for the Pennsylvania specimen were given as "Pennsylvanie, H. G. Klages" but for the Texas specimen no collection data were given. The latter he said was given to him from the Stockholm Museum as one of the examples attributed by Stål to R. fusca.

Pennsylvania is well within the range of the nominate subspecies but Texas is not, and it is likely that the specimen from the latter is $R$. australis Hungerford (1922: 449). It is remotely possible that the Pennsylvania specimen is $R$. buenoi Hungerford (1922:442), although it seems unlikely that Montandon, a careful worker, would have overlooked the profound sulcus on the prothoracic ventor of buenoi. Both australis and buenoi were described twelve years after Montandon's edentula, and both of the former names are now well established in the literature. Because varieties described before 1960 have standing as species group names according to the 1985 Code of the ICZN, the names australis and buenoi are at risk as possible junior synonyms of edentula unless the latter is definitely established to be a variety of fusca. Further, Sites and Polhemus (1994) have prepared a review of this group in an effort to stabilize the nomenclature of North American Ranatra, establishing the variety edentula (sensu Hungerford, 1922) as a junior synonym of fusca.

Two specimens of $R$. fusca from Pennsylvania collected by Klages were loaned by the Carnegie Museum of Natural History. Neither of these has the reduced distal tooth of the fore femur, thus neither is suitable for a neotype of edentula. It is likely however that Montandon's specimen came from this series. The expression of the femoral tooth is variable within series as noted by Hungerford (1922), who questioned the validity of the variety edentula, and by Sites and Polhemus (1994) who found a
complete size range of distal fore femoral teeth in a single long series from Colorado, from very weak to very pronounced.

Texas specimens of $R$. australis received from the Swedish Museum of Natural History, collected by Belfrage, were held under R. fusca in that collection, and one bears a label in Montandon's handwriting "Ranatra fusca Pall d. B., A. L. Montandon 97." Dr. Per Lindskog (pers. comm.) believes that the Texas specimen of R. americana edentula came from this series, but this is conjecture until we find the specimen labelled as such by Montandon. Montandon was confused about the true identity of R. fusca and in 1910 gave it the unnecessary new name R. americana. It remained for Hungerford (1922) to establish firmly the identity of R. fusca.

Horn and Kahle (1936) state that Montandon sold his collection of Cryptocerata (water bugs) to the British Museum, but it is not clear whether this sale included material only up to 1901 , or to 1911. The types of $R$. americana edentula are not in that museum according to the curatorial staff. Dr. I. M. Kerzhner (pers. comm.) says that Montandon sold various parts of his water bug collection at different times, but that the species described during the latter part of his working career (which declined after 1913) were mostly held in the "Grigore Antipa" Museum of Natural History, Bucharest. A single specimen of $R$. australis Hungerford was received from this museum, labelled "Texas," and identified by Montandon as $R$. fusca, and the curator Dr. Stanescu informs me that there is no material of $R$. americana edentula in that museum. Mr. I. Sienkiewicz (1964) prepared a catalog of the A. L. Montandon Collection of Palaearctic Heteroptera preserved in this museum, but the promised catalog of the remainder of the collection was never published. Mr. Sienkiewicz says that he has no further information on the Nepomorpha of Montandon.

I believe that the unsuccessful search for the type material of Ranatra americana edentula Montandon, which involved the major museums of North America and Europe, plus the measures described above, justify the designation of a neotype. A neotype is therefore designated here for Ranatra americana edentula Montandon (=Ranatra fusca edentula Montandon; see synonymy above), and the type locality is restricted to Pennsylvania. This action is justified by the need to stabilize the nomenclature for the species Ranatra fusca Palisot de Beauvois and R. australis Hungerford. The neotype chosen, a male collected in Pennsylvania, bears the following labels: 1) A handwritten label "Travers Creek, Beaver Co., Pa., VII.21.1933"; 2) A printed label "Ranatra fusca Palisot Beauvois, Det. D. V. Bennett"; 3) A pink handwritten label "NEOTYPE, Ranatra americana edentula Montandon, J. T. Polhemus 1993." The neotype is of the opposite sex from that described by Montandon because the "edentula" form is not present in the females available from Pennsylvania; this choice is permitted by the 1985 Code [75 (d) (4)]. The neotype has been placed in the Carnegie Museum of Natural History.-John T. Polhemus, University of Colorado Museum, 3115 S. York St., Englewood, Colorado 80110.

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## PREDATION BY CLIVINEMA COALINGA BLIVEN (HETEROPTERA: MIRIDAE: DERAEOCORINAE: CLIVINEMINI) OF ORTHEZIA ANNAE COCKERELL (STERNORRHYNCHA: ORTHEZIIDAE)

Knight (1928:34) mentioned that Clivinema sericea Knight is a predator of Orthezia sp., quoting unattributed label data of the type series. He also suggested that some members of the genus must be predators of scales and mealybugs (Knight, 1928:36). Other mention of Clivinema is restricted to descriptions of included taxa (see Van Duzee, 1917:363; Henry and Froeschner, 1988:273). Therefore, a biological observation of another species is presented.

On 29 April 1980 RSM observed a population of Orthezia annae Cockerell on Atriplex polycarpa (Torr.) Wats. in the remnants of a San Joaquin saltbush community (Barbour and Major, 1977) at Kettleman City, Kings Co., California. Close examination revealed mirids, Clivinema coalinga Bliven (1966), which initially were not readily apparent among the similarly colored scales. A sample of the scale, its host, and the mirid were placed in a collection container and taken back to the lab. The next morning the mirid adults and nymphs were observed feeding on the scales. RSM returned to the same locality on 20 May 1980 and confirmed that C. coalinga is a predator of Orthezia scales under natural conditions.

Voucher specimens of $C$. coalinga are in the collections of Texas A\&M University (TAMU), the American Museum of Natural History (AMNH), and RSM. Scale
vouchers are in the RSM collection. We wish to thank Dr. Joseph Schaffner, Department of Entomology, Texas A\&M University, for the initial generic determi-nation.-Richard S. Miller, Department of Entomology, Montana State University, Bozeman, Montana 59715 USA and Randall T. Schuh, Department of Entomology, American Museum of Natural History, New York, New York 10024 USA.

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## MEGATOMA (PSEUDOHADROTOMA) KALIKI (COLEOPTERA: DERMESTIDAE): RANGE EXTENSION AND CHARACTER VARIATION

Megatoma (Pseudohadrotoma) kaliki (Beal, 1967) has been known only from the 3 specimens of the type series from British Columbia. A number of additional specimens extends the range along the Rocky Mountains as far south as southwestern Colorado. The data are as follows. COLORADO: La Plata Co.: Durango, 2-vii-1990 (K. Hepworth). IDAHO: Latah Co.: Moscow Mt., 17-vii-81 (R. Turnbow). MONTANA: Gallatin Co.: Bozeman, 16, 26, 30-vi-87 (D. L. Gustafson); ibid., 11-vii-87 (D. L. Gustafson), ibid., 1-vii-21-x-88 (funnel trap, D. L. Gustafson); Blackmore Creek, 7,200 feet elev., 8-vi-26-ix-89 (interception trap, D. L. Gustafson); Bridger Creek, 1, 3, 24, 30-vii-87 (D. L. Gustafson); ibid., 9-viii-87 (D. L. Gustafson); Bozeman Creek, 23-vii-4-ix-89 (funnel trap, D. L. Gustafson); Gallatin Canyon, 31-vii-54 (R. C. Froeschner); Langhor Campground, Hyalite Creek, 10 miles south Bozeman, 3-viii-24-ix-89 (funnel trap, C. E. Seibert); Squaw Creek, Spire Rock Campground, Gallatin Canyon, 15 -vi-12-vii-88 (funnel trap, C. E. Seibert). Madison Co., 4-vi-22-vii-89 (funnel trap, D. L. Gustafson).

Specimens of the type series lack a median ocellus, "probably a good specific character," according to the original description (Beal, 1967, Misc. Publ. Ent. Soc. Am. 5(6):281-312). The specimen from northern Idaho lacks a median ocellus. Of
the 26 Montana specimens from adjacent Madison and Gallatin counties, 4 lack a median ocellus, 6 possess a reduced ocellus, and 16 have a fully developed ocellus. Four females taken from Durango, La Plata Co., Colorado, have a median ocellus. A specimen from Evergreen, Jefferson Co., Colorado, which I tentatively assigned to $P$. perversa (Fall) because it possesses a median ocellus (Beal, 1967, op. cit.), most certainly also belongs to this species. In other respects specimens of the species fall within the range of variation described for the type series, except that lengths of females vary from 2.7 to 4.0 mm , and the ratio of width (across humeri) to length (of pronotum and elytra) of females varies from 1:2.14 to 1:2.35.

The specimens collected in funnel traps were taken in unbaited Lindgren traps (Michael Ivie, pers. comm.). The Durango, Colorado, specimens were taken in a home.-R. S. Beal, Jr., 1094 Pine County Court, Prescott, Arizona 86303.

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## A SOUTHERN DISTRIBUTION FOR THE INTRODUCED DUNG BEETLE APHODIUS (OTOPHORUS) HAEMORRHOIDALIS (L., 1758)

Aphodius haemorrhoidalis is a bovine dung specialist species which frequently occurs in north and south European grasslands (Dellacasa, 1983; Hanski, 1991; Lumaret and Kirk, 1991). It is one among many other European species accidentally introduced in North America (Blume, 1985). In this continent it is commonly found in the field in dense populations (Kessler and Balsbaugh, 1972; Merrit, 1974; Mohr, 1943).

In 1915 Schaeffer reported A. haemorrhoidalis for the first time in New Jersey, United States (in Woodruff, 1973). About 1940 this species enlarged its geographical range to New York, Nova Scotia, New Brunswick, Quebec, North Carolina, South Carolina and Illinois. In 1960 it was collected in Kentucky and Massachusetts; and in British Columbia and Florida in 1967. This last record is the southernmost and it possibly represents the initial dispersal of this beetle southward (Woodruff, op. cit). According to Brown (1967) who reported it from British Columbia, A. haemorrhoidalis had already spread to the northwest. Recently it has also been reported from Nebraska (Ratcliffe, 1991).

On September 29, 1993 we have caught two specimens of this species trapping with cow dung in pasturelands at the state of Durango (Mexico): El Tapado (Biosphere

Reserve of Mapimí, 40 km NE from Ceballos). This is the first known record south of Rio Bravo, and the southern known boundary of the species range. In addition to A. haemorrhoidalis, we found in the Mapimí grasslands three other species introduced in North America: Digitonthophagus gazella (Fabricius), Euoniticellus intermedius (Reiche) and Aphodius lividus (Olivier); another probably introduced, Aphodius nigrita Fabricius; and only one native dung beetle, Canthon (Boreocanthon) puncticollis LeConte.-Jorge M. Lobo, Museo Nacional de Ciencias Naturales (C.S.I.C.), Dept. Biodiversidad, c/ José Gutiérrez Abascal, 2. 28006, Madrid, Spain.

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## BOOK REVIEWS

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Behaviour and Social Evolution of Wasps: The Communal Aggregation Hypothesis. Y. Itô. 1993. Oxford University Press, Oxford. viii +159 pp. £13.50 paperback, £30 cloth.

This book is essentially one argument, and at 134 pages of text, it is not one long argument. Itô argues for the central role of mutualism in the evolution of social behavior, over that of kin selection. Specifically, he cites the common presence of multiple egg-layers ("queens"), and concludes that "intracolony relatedness is likely to be low for these species. Thus, more attention must be paid to mutualism" (p. 2).

Wasps display two types of polygyny. In species in which females found colonies independently, there may nevertheless be "foundress associations" of multiple egglayers. These associations have generally been considered temporary, with one female eventually becoming the predominant egg-layer, leading to "functional monogyny." Some tropical species found colonies by swarms containing multiple egg-layers and permanently sterile workers. This latter type of polygyny is usually considered to be permanent, although the number of queens may be reduced during the colony cycle, producing "cyclical oligogyny" (see West-Eberhard, 1978a; Queller et al., 1993a; Strassmann et al., 1991, 1992). West-Eberhard (1978b) presented a hypothesis for the origin of social behavior by mutualistic associations of initially casteless females, with subsequent evolution of reproductive dominance leading to castes. She proposed that the polygyny of swarm-founding species most commonly evolved from the condition of functional monogyny, but did not rule out the possibility of a direct transition from a stage of primary polygyny with only rudimentary castes. In 1989, I placed this argument in a phylogenetic context, mapping behavioral traits onto cladograms for all the social wasps (see also Carpenter, 1991, 1992). The endemic Oriental subfamily Stenogastrinae, sister-group to the Polistinae + Vespinae, founds colonies independently and displays temporary reproductive division of labor. My analysis indicated that this condition is the ancestral social organization. The phylogenetically most basal polistine genus, Polistes, also founds colonies independently, but has permanent reproductive division of labor. This is also the case in the next most basal genus, Mischocyttarus. Genera that display swarm-founding polygyny are relatively more apical; the condition is more restricted in its phylogenetic distribution. This led to the conclusion that swarm-founding polygyny is secondary, and evolved from functional monogyny.

Itô takes issue with this conclusion. He cites especially his own studies on the independent-founding genera Polistes, Mischocyttarus and Ropalidia, showing cases of multiple egg-layers among foundresses of colonies. Although admitting that many species in these genera are monogynous or functionally monogynous, and not adducing any data on genetic relatedness, he cites a low frequency of dominance behaviors among the cofoundresses in various species, and dismisses the possibility of functional monogyny, concluding that relatedness must be low in such cases. He argues that social cohesion is brought about by mutualism, citing data showing higher
failure rates for colonies founded by single females than by foundress associations. The benefits of nesting in groups are thus seen as greatly outweighing the costs to individual reproduction. While admitting that evidence is incomplete or lacking, he suggests that castes evolved from foundress groups that manipulated progeny into becoming workers, and that swarm-founding polygyny evolved directly from this condition, without an intervening stage of functional monogyny.

His argument fails on two counts. First, he has no phylogenetic perspective. Itô considers that the genera he studied are variable in whether they are monogynous or polygynous, but does not establish the groundplan condition in any of the taxa. The polygyny he sees as primary could thus be secondary; he presents no evidence either way. The second failure is worse: the available genetic data controvert his argument. He includes the paper by Strassmann et al. (1989) in his references, but he does not discuss this paper in the text. Strassmann et al. (1989) listed coefficients of relatedness for 14 species of polistines. These ranged from 0.3 to 0.8 , with a mean more than the 0.5 value for relatedness to offspring. Two of these species, Polistes versicolor and Mischocyttarus basimacula, were among the taxa shown by Itô to have multiple egg-layers; their coefficients of relatedness, however, were $0.371 \pm 0.084$ and $0.435 \pm 0.116$, respectively (see also Queller et al., 1992). As Queller et al. (1992: 87) concluded regarding Mischocyttarus basimacula: "relatedness was too high to allow for very many egg-layers. Our data tend to support the conventional view that one female is usually able to dominate the others." Moreover, relatedness values for swarm-founding polygynous species tend to be lower; the three species listed in Queller et al. (1988) ranged from 0.1 to 0.3 for workers, the two species reported by West-Eberhard (1990) and Strassmann et al. (1992) were 0.2, and the species added by Queller et al. (1993b) 0.5 -but relatedness among queens was higher.

The relatively higher relatedness found in the independent-founding polistines supports the inference that functional monogyny characterized the phylogenetically most basal elements of the Polistinae, and was ancestral (see also Ross and Carpenter, 1991). Itô's conclusion may thus be rejected, but this is not to say that all parts of his argument are entirely wrong. Frequency of subordinate, joining behavior does not correlate with relatedness in Polistes (Hughes et al., 1993). Mutualism is generally accepted as crucial in the origin of group nesting in the first place (West-Eberhard, 1978a), and advantage obtains to group nesting regardless of relatedness (Wenzel and Pickering, 1991). Such mutualism has evidently operated together with kin selection in the evolution of social behavior in wasps. Even as a critic, I agree with the author's list of desiderata for further study (p. 134), and join him in hoping that his book stimulates work along these lines.-James M. Carpenter, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.

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The Insects of Macau. - E. R. Easton. March 1993. University of Macau Publications Centre, Taipa, Macau. 58 pp., paper. HK\$100 (ca. US\$12.82), including air postage and handling. 1,000 copies printed; no ISBN.

Macau (English Macao, Mandarin Aomen) is the oldest European settlement in the Far East, but unlike Hong Kong, its boisterous neighbor 27 km east across the mouth of the Pearl (Zhujiang) River, Macau has never been a colony and was not won at gunpoint. Rather, this tiny outpost has persisted for over four centuries under the benign administration of the Portuguese, who make no claim to ownership. It
shows: few cities in Asia are more tranquil or attractive. Indeed, were it not for the faces of the people ( $97-99 \%$ Chinese, depending on mainland political conditions), a visitor gazing out at the South China Sea from one of Macau's luxuriant verandahs might well imagine himself transported to Madeira or some similar comfy hideaway. And for visiting entomologists there is now this book, "the first published work of any size . . . on the insect fauna of Macau" (p. 5).

The territory encompassed by this guide is minuscule. Macau proper is a narrow peninsula scarcely 5 sq km in area, but it is linked to the rocky, verdant islands of Taipa ( 3.4 sq km ) and Coloane ( 7.2 sq km ) by bridge and causeway. On the north shore of Taipa Island is the University of Macau (formerly the University of East Asia), and it is here that Dr. Emmett R. ("Slim") Easton has been observing insects since his arrival in 1989 on a visiting professorship.

The body of this book comprises descriptions and color photographs of 51 large, showy, or unusual insects-the species most likely to be noticed even by those with no particular interest in entomology. These are assigned to 27 families (number of species in parentheses): Gryllotalpidae (1), Gryllidae (1), Mantidae (2), Blattidae (2), Reduviidae (1), Pentatomidae (4), Largidae (1), Fulgoridae (1), Cicadidae (4), Pieridae (1), Danaidae (2), Papilionidae (4), Sphingidae (4), Geometridae (1), Arctiidae (2), Noctuidae (1), Syrphidae (1), Vespidae (2), Apidae (2), Carabidae (1), Buprestidae (1), Cerambycidae (4), Meloidae (1), Dytiscidae (1), Elateridae (1), Scarabaeidae (4), and Lucanidae (1). Authorities differ concerning the familial status of the largid Physopelta gutta; some (e.g., Hill et al., 1982, Insects of Hong Kong) consider this species a pyrrhocorid. Also, Easton has adopted the current broad classification of the Arctiidae, wherein the Amatidae (Syntomidae, Ctenuchidae) is reduced to a subfamily (Ctenuchinae). Unfortunately, the text is marred throughout by multitudinous typographical errors (e.g., "Portugese"), uncouth abbreviations (e.g., "P.R.O. China"), and outrageous (some would say laughable) run-on sentences that presumably only reflect the difficulties attending publication in a Cantonese-cum-Portuguese-cum-English environment.

Considering the meager resources available to its author, this book is something of an accomplishment. A large format ( $19 \times 27 \mathrm{~cm}$ ) and heavy, glossy paper complement the photos, which range from good to fair (several are too dark, obscured by shadows, or out of focus). As well, there is a great deal of information-gained firsthand-on host plants, mating behavior, development, and voltinism. But sensitive readers will be most drawn to Easton's numerous anecdota, among them: scrounging for burrows of the cricket Brachytrupes portentosus in the United Chinese Cemetery (p. 8); accounting for the abundance of the hematophagous reduviid Triatoma rubrofasciata near a campus garbage collection site, a harborage for rats (p. 13); recording the songs of Macau's several cicadas, still common in "hilltop forests" of Taipa and Coloane, while recalling how a prominent Chinese physician (Shi Jinmo, 1881-1969) combined the exuviae of one species (Huechys sanguinea) with ground magnetite, sea shells, and a number of plant products to treat hypertension (p. 20); reasoning from bird attacks that the aposematically colored geometrid Obeidia tigrata is nonpoisonous (p. 35); remarking on the Chinese predilection for fried diving beetles (Cybister tripunctulatus) (p. 51); and speculating as to whether construction of a golf course on Coloane will benefit a local scarab (Protaetia orientalis) (p. 55).

It would be a disservice to conclude this review without reminiscing somewhat on

Dr. Easton's extraordinary career. Born in Bradford, Pennsylvania, he earned his B.S. at Penn State but soon thereafter left for Texas A\&M University, where he acquired both his M.S. and the apt sobriquet "Slim" (which he fosters to this day). Then on to Oregon State, where this writer first met him wrestling with an impossible full-time teaching schedule and pursuing, with passion bordering on obstinacy, his professional focus: ectoparasites. Slim's scientific exploits while in Oregon have duly passed into legend. A real-life Indiana Jones of entomology, he would hurl himself from the merest dinghy onto Oregon's awesome coastal cliffs, scaling these for the sole purpose of collecting lice, fleas, flies and acarines from resident sea birds (1970, J. Med. Ent. 7:438-445). On the opposite side of the state, well past midnight, he could be found scouring the back roads of the badlands, ever vigilant for pocket mice, kangaroo rats, and their arthropod associates. Award of the doctorate only fueled his wanderlust. He immediately left for Tanzania, where he spent the better part of five years as an animal health officer, often under inimical conditions. With the fortitude of a Voortrekker, he sought out and rediscovered Nuttalliella namaqua (Nuttalliellidae), the so-called missing link between argasid and ixodid ticks and a species known from only 13 specimens since its description by Bedford in 1931 (Parasitology 23:230-232). This achievement, more than any other, established Easton's reputation as an indefatigable field entomologist. Perhaps out of breath, he chose to spend the next 12 years as an Associate Professor at South Dakota State University, but when that institution's Plant Science Department summarily folded, Slim armed himself with a Fulbright scholarship, spun the globe, and found his finger pointing at Port Moresby and the University of Papua New Guinea. There he continued his ectoparasitological investigations, despite increasingly ominous sociopolitical rumblings, before settling at last amid the comparative comforts of Macau. During two decades of turbulence, he had somehow also found time to publish over 100 scientific papers and reports.

In the last five years, Slim Easton has prepared about a dozen manuscripts on Macau's natural history. But what of the future? Sometime in late 1999 the Portuguese flag will be lowered forever along the Avenida de Almeida Ribeiro, and Macau's fate will join with that of the People's Republic of China. To their lasting credit, the Portuguese have accorded virtually all native Macanese (some 400,000 souls) the right to return with them to the land of Dom Enrique and Vasco da Gama. Might there also be room for one productive expatriate American? Those who know him will hardly be surprised if "Old Slim" succeeds in trading Taipa for the Tagus. Boa sorte, meu colega! Boa viagem! - Richard G. Robbins, Armed Forces Pest Management Board, Walter Reed Army Medical Center, Washington, D.C. 20307.
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Proceedings of the Second International Congress of Dipterology.-L. Weisman, I. Országh and A. C. Pont (eds.). SPB Academic Publishing, The Hague, Netherlands. 1991. 367 pp. cloth. $\$ 82$.

Considering that the Diptera are one of the largest and economically and medically most important orders of insects, and that many entomologists study their biology
and systematics, it may come as a surprise that there is not a long history of "International Congresses of Dipterology." Indeed, until today only two such meetings were organized.* Both were held in eastern European countries with the last one taking place in Bratislava in 1990. More than 270 dipterists presented their research in numerous talks and on a fair number of posters. If the quality of the selected papers in this volume is any indication for the quality of Diptera research, I am looking forward to attending many more meetings. I was generally impressed by the ability of most authors of the research, as well as the review papers, to summarize efficiently their findings and yet at the same time to present an overview of the relevant literature.

Being a systematist, I was initially reluctant to read any of the applied entomology papers. However, as a reviewer I felt obliged at least to get an impression. I ended up reading almost all papers in the book. As expected, some were much less rewarding than others but, overall, the quality was excellent. There is a very definite trend within applied entomology to avoid using large quantities of pesticides. There appear to be rather different strategies for the control of blood sucking and phytophagous Diptera. For blood-sucking flies various strains of Bacillus thuringiensis and sphaericus are both cost-effective and efficient. A number of case studies are described in Becker's paper. However, it was disconcerting to learn that Culicoides defies such strategies because of the "lack of any parasporal inclusion activation in the larval midgut" (Kremer et al.). Maybe traps supplied with octenol and carbon dioxide will be useful for the control of Culicoides as it apparently is for many nematoceran bloodsuckers (Becker, Kline). Sometimes I was intrigued only by details. Who would have guessed that 83,000 to 163,000 tabanids would have to be interrupted during feeding and afterwards feed on another human being before a single case of transmission of the AIDS virus would be likely? As little as 10 nl of blood remains in the mouthparts of tabanids disturbed during feeding (Anderson).

For phytophagous Diptera authors feel that some pesticide use is inevitable and their efforts are concentrated on reducing the amount of chemicals used (Finch). They are either deployed more specifically to the target organ of the dipteran attack or the "pest" species is repelled from the host by using species specific deterrents (e.g., some oviposition deterrents produced by tephritids themselves or plant compounds (Kline)) or resistant strains of the host (Finch).

There were also a good number of interesting systematics papers. Some revolved around the various hypotheses regarding homologies of the sclerites found in male terminalia. Wood's clearly reasoned analysis of the homologies of the male terminalia will hopefully set standards for some time to come. Even if one were to disagree with his modified "epandrial hypothesis," one would hope that conflicting views are presented in a similarly cogent style. The manuscript certainly benefitted tremendously from Idema's excellent illustrations whose color codings made it easy to identify putatively homologous structures across taxa. Wood's paper is a must for all Diptera systematists interested in higher level relationships. Griffiths, a proponent of the "periandrial hypothesis," summarized the current knowledge of homologies of the muscles found in male terminalia. Unfortunately, it was very difficult to follow

[^7]his discussion without consulting the primary literature for illustrations. No figures were provided.

While the contributions of Wood and Griffiths addressed problems of the higher level relationships among Diptera, Grimaldi presented a summary of his results of a phylogenetic analysis of the Drosophilidae based on 167 species and 217 characters. For some time to come, his cladistic analysis will set standards for any work on the drosophilids and replace Throckmorton's and Okada's hypotheses that were either based on intuition or phenetic techniques. Not surprisingly, the analysis found that Drosophila is paraphyletic unless a number of subgenera are sunk. Also of particular importance was the finding that all Hawaiian Drosophila species (now belonging to the genus Idiomyia) form a monophyletic group which is presumably much older than the Hawaiian islands that are currently above sealevel. These results will have a profound impact on studies of the adaptive radiation of Hawaiian fruit flies.

Two additional systematics papers (Marshall, von Tschirnhaus) demonstrated that as soon as Neotropical species are studied the geographic distribution of genera may change dramatically. Marshall found that a genus of Sphaeroceridae (Sclerocoelus) that was primarily known from the Nearctic was in fact mainly Neotropical. On one field trip von Tschirnhaus discovered 20 new species in a fairly small genus of agromyzids at one site in Peru (Phytobia) and suddenly $33 \%$ of all species were neotropical. Also quite interesting was von Tschirnhaus's account of how electrolytes on washing lines attracted a large number of males of agromyzid species at that Peruvian collecting site. Most species turned out to be undescribed and one can only wonder whether they may have come from the canopy where agromyzids, hitherto considered to be a cold climate loving family, may be rather diverse.

A common theme in a number of the systematics papers (e.g., Grimaldi, Mathis) was a critique of faunal studies. All too often such studies are bound to create synonyms and their contribution to the understanding of Diptera systematics is very limited. This point is well illustrated by the few faunistic papers published in this volume. They were among the least interesting contributions because species lists alone are not very informative.

If there was anything resembling a common concern expressed throughout the whole volume, it was certainly that there is a lack of recent comprehensive systematic studies. Our knowledge of Diptera is extremely limited, with not even the taxa that are notorious for their medical and economic importance having seen modern revisions. Thus, applied entomologists as well as ecologists face the same problems. Be it that Hövemeyer was unable to evaluate the catches of his emergence traps because the species could not be identified or White's finding that much money and effort had been wasted on trying to control a composite weed using the wrong species of tephritids belonging to a sibling species complex. Considering that in Germany up to $50 \%$ of the dipteran species are considered endangered (Vogel) without making it onto the red lists of endangered species, not much time remains to study the diversity of many geographic areas.
Similarly common was a quest for more work on larvae. Several authors pointed out that from an ecological point of view larvae are the more important life stage of many Diptera (Hövemeyer, Zuska) and the adults are little more than the conspicuous flying ovaries and testes. Applied entomologists (White) expressed interest in being able to recognize the immature stages for an early identification of pest species as well as for the control of imported plant material. Systematists were obviously in-
terested in having an independent (Krivosheina) data set to test their phylogenetic hypotheses.

The format of the book is dissatisfactory. For example, apparently there was no agreement on whether an abstract should be provided at all and, if so, where it should be placed. The book is not organized by subject matter. Instead the papers appear in the alphabetical order of the authors' names. The quality of the printing is surprisingly uneven. Idema's color coded plates are very competently reproduced (however, rumors have it that they were printed in Canada). On the other hand the book was printed using photo offset and a more attractive font would have made quite a difference. The quality of the paper is rather poor and the photos and some text on pages adjacent to illustrations are printed on a different kind. Considering the very high price of $\$ 82$, more attention should have been paid to editorial details and the layout. - Rudolf Meier, Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853, USA and Institut für Zoologie, FU Berlin, AG Evolutionsbiologie, Königin-Luise-Str. 1-3, 14195 Berlin, GERMANY.
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Nymphs of North American Stonefly Genera (Plecoptera). - Kenneth W. Stewart and Bill P. Stark with illustrations by Jean A. Stanger. 1988. Thomas Say Foundation, v. 12. University of North Texas Press, Denton, Texas. xiii +460 pp. $\$ 35.50$ paper.

Some 57 years after the publication of Claassen's (1931) "Plecoptera Nymphs of North America (North of Mexico)," the subject is updated with Stewart and Stark's "Nymphs of the North American Stonefly." With this recent study, which includes literature published through 1987, the total number of North American Plecoptera is elevated from 21 to 99 . In terms of content, purpose, and style, Stewart and Stark's book is reminiscent of Wiggins' elegant book on the genera of North American caddishfly larvae (1977). Stewart and Stark, however, present more extensive and comprehensive information especially on the subjects of ecology, behavior and life cycles.

The introductory chapters of this book include sections on classification and phylogeny, biogeography, nymph ecology and behavior, morphology, and adaptation. The phylogeny section lists several competing phylogenies of stoneflies, but mainly discusses studies by Zwick $(1973,1980)$ and Nelson (1984). Stewart and Stark advocate Zwick's phylogeny over Nelson's which is more recent and modern, i.e., computer assisted. Their preference for Zwick's classification amounts to its being "the most complete" which may or may not be the most natural classification. They acknowledge, however, that none of the current plecopteran classification systems are completely satisfactory due to absence of a thorough analysis of both larval and adult characters.

The authors put a great deal of emphasis on the ecology and behavior chapter which includes many tables and graphs. This chapter specifically covers: life cycles and voltanism, egg development, nymphal growth and development, food habits, feeding, trophic interactions, habitats and space partitioning, secondary production,
and stonefly management. The literature review on these subjects is extensive. The morphology section, especially the character discussion using SEM pictures and drawings of mouthparts, is potentially useful and readily available for future phylogenetic analysis.

The final chapters (2/3) of this book are devoted to the systematics of North American Plecoptera. These chapters start with a key to the families of the nymphs of North American Plecoptera. Each family begins with an introductory section followed by a generic key. All the genera are arranged alphabetically. In addition to life history presented in the introductory chapters, the authors provide detailed information regarding previous nymph descriptions and illustrations, nymph morphology and biology for each genus.

There is no doubt that a study such as this could only be successfully presented with appropriate illustrations. There are 99 full pages of habitus pictures, one for each genus, and 99 additional illustrations of mouth parts, gills, cerci, legs, and other characteristics. Most of these were drawn by Jean A. Stanger.

Individually habitus pictures are beautifully drawn, but collectively, they lack the consistency of clarity and style that we see in Wiggins' wonderfully presented pen and ink work. Some seem to show more detail while others are too light (e.g., figs. $8.13,9.9$ ) which render them much paler in comparison. One habitus drawing (fig. 11.13) by R. F. Surdick stands out because it is very different from the remaining habitus drawings.

Overall, there are a few minor deficiencies pertaining to the drawings. For example, the tips of the antennae and cerci of each habitus are cut off and therefore do not show actual length in reference to total body length. Additionally, it is not clear why the authors placed separate drawings of head and pronotum for most genera when the same features are shown, generally without much difference, in the habitus drawings (e.g., figs. 14.1 and 14.2 A , and 14.19 and 14.20A). Some of the slight differences between the habitus, and head and pronotal drawings (e.g., figs. 7.9 and 7.10 A ) may be an artifact of the different technique used, i.e., carbon dust vs. pen and ink, respectively. In contrast, some of the differences between habitus, and head and pronotal drawings are clear and probably intended to show variation. These drawings, however, are showing variations within species which is not discussed since it is beyond the scope of this book.

Some nomenclatural information is either missing or difficult to find. For example, references for date and source of the original descriptions are missing for each genus and type species. Although a general discussion of nomenclature for each family and a list of name changes for each genus are provided, it is difficult to trace when a particular taxonomic change in rank and name is made and by whom. I noticed only one typographic error, the table 2.1, family Perlodinae should be corrected as Perlodidae.

In spite of these minor deficiencies, this book is highly recommended and a welcome addition to the freshwater sciences. It is, undoubtedly, a useful and comprehensive reference book regarding nymph identification, taxonomy, classification, ecology, behavior, and natural history of Plecoptera focusing mainly on North American fauna. The authors' many years of effort in rearing nymphs both in the lab and in their natural habitat should be commended. Their use of different methods for rearing and gathering new information on the biology of plecopterans are very encouraging and hopefully will stimulate interest in other biologists. Hopefully, this
book will stimulate further research in plecopteran phylogeny, as well as other related disciplines. - Sule Oygur, Dept. of Entomology. American Museum of Natural History, New York, New York 10024-5192.

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J. New York Entomol. Soc. 102(3):396-397, 1994

Verzeichnis der Sandlaufkäfer der Welt (Coleoptera, Cicindelidae [Checklist of the Tiger Beetles of the World (Coleoptera, Cicindelidae)]).-Jürgen Wiesner, 1993. Hago-Druck, Karlsrud-Ittersbach Verlag Erna Bauer, Siedlung 15, 7538 KelternWeiler, Germany, 364 pp . Price: US $\$ 75.00$ plus $\$ 5.00$ postage and handling from Sciences Naturelles, 2 rue Mellene, 60200 Venette, France.

My first reaction to reading the announcement of Jürgen Wiesner's catalogue was to question if our present state of knowledge of tiger beetle systematics and distribution warranted so ambitious a project. My answer? Yes and no. Not since Walther Horn's treatise (1908, 1910, 1915, Genera Insectorum 82: 487 pp. ), monumental still, has anyone attempted a work of such scope. Wiesner's work is a foundation on which to build.

Wiesner's catalogue consists of a Foreword in German and English (p. 6), a systematic section (pp. 7-230), literature citations into 1992 (pp. 231-274), an alphabetical index (pp. 275-343), and an index (pp. 344-364).

The most positive uses of the catalogue are its ease of use and concentration of information. Different print sizes and spacing permit easy scanning. Each section is a high point: the systematic section with references, subspecies, synonymies, and ranges; the literature section with citations through at least early 1992; the alphabetical index with all names cited from family to subspecies and varieties, recognized names in bold print and cross-referenced to the associated genus or species, and synonyms in small print and cross-referenced to their proper taxon; and a systematic index which serves excellently as a checklist.

There are some detractions in the book, some that should be corrected in future editions, and some that counter my own personal preference. None interferes with the book's overall excellence.

1. Typographical errors are few so I am uncertain if spellings such as Platychile, Picnochile, and Ropaloteres are lapsi or intended as I have neither researched the original citations nor am I fluent in the niceties of Greek etymology. The spelling
of -cheila (Greek: lip) is inconsistent being rendered severally as -cheila, -chila, or chile (e.g., Amblycheila, Neochila, and Platychile respectively).
2. Despite Article 36a of the International Code of Zoological Nomenclature, 3rd edition, 1985, Wiesner credits authorship of nomotypic ranks between subfamily and subtribe to others than Latreille for Cicindelidae Latreille 1806 (e.g., Cicindelinae Csiki 1906, Cicindelini Sloane 1906, and Cicindelina W. Horn 1908). Latreille is the author of all four names.
3. Theses and dissertations, although not constituting formal publication, do contain valuable information. Several from the United States and Canada and widely quoted in the literature were not cited by Wiesner. I do not personally accept the philosophy of some that an author is not obligated to refer to a given available source.
4. Wiesner uses species-groups inconsistently. Among others, Ctenostoma, Tricondyla, Collyris, Megacephala, and Therates are so divided but Cicindela, quite established in the literature (e.g., Rivalier's subdivisions of his subgenus Cicindela), is not.
5. In listings of subspecies under a given species, Wiesner does not give the nominate subspecies its own lower case letter. Personally, I would number the nominate subspecies " $a$ " and each succeeding subspecies " $b$," etc.
6. The English version of the Introduction is replete with grammatical errors, some phrases so incomprehensible to me that I needed to read the German version. Wiesner must have this section carefully proof-read for future editions.

Despite the daunting price, Wiesner's contribution is invaluable to every student of tiger beetle systematics. I have happily converted his systematic index into a checklist for curatorial purposes. The wealth of literature listings greatly reduces my time for gathering sources. Anyone studying any sort of comparative biology of any series of species can determine instantly how those species may be interrelated. My heartfelt thanks go to Dr. Wiesner for his work and my hope as well that the next edition will have the minor flaws eliminated.-Sanford Leffler, 4701 15th Av . $N E$, \#6, Seattle, Washington 98105.
J. New York Entomol. Soc. 102(3):397-399, 1994

Biology and Conservation of the Monarch Butterfly. - Stephen B. Malcolm and Myron P. Zalucki, editors. 1993. Natural History Museum of Los Angeles Science Series no. 38. Los Angeles, California. 419 pp. Price: $\$ 90.00$ (cloth).

The natural history of the monarch butterfly (Nymphalidae, Danainae, Danaus plexippus, L.) has without doubt been more thoroughly studied than that of any other insect, if not any living thing. The monarch has been a model organism in studies of mimicry, ecological chemistry, migration and overwintering biology and its subfamily is one of the few butterfly groups with a robust phylogenetic hypothesis of relationships (Ackery and Vane-Wright, 1984). It is also probable that the monarch is the only economically unimportant insect to have had two international symposia devoted to its biology and conservation. This book is the proceedings of the Second International Conference on the Monarch Butterfly, or "Moncon 2," held at the Los Angeles County Museum on 2-5 September 1986.

The book succeeds admirably in most aspects as a conference proceedings volume. Although it is a collection of original papers on primary research by 50 authors, there is considerable continuity of style and quality among the individual contributions. The production quality of the text, tables and figures is as high as one would expect to see in a first-rank journal. The editors have divided the papers into sensible subdisciplinary categories, and written useful introductory and concluding remarks that explain the book's structure and highlight the various authors' salient points. Each section is headed by a full-page plate (two are in color) illustrating diverse aspects of monarch biology. The sections are as follows:

Systematics: one paper on the evolutionary origins of the monarch from a phylogenetic perspective.

Chemical Communication: three papers addressing pheromones and the controversial role of pyrrolizidine alkaloids in courtship and defense.

Mating Behavior: three papers, including Van Hook, which demonstrate surprising reverse-assortative mating in Mexican overwintering colonies.

Host Plant Use, Cardenolide Sequestration, and Defense against Natural Enemies: six papers, ranging from phylogenetic analysis of host plant use to quantitative models of cardenolide storage by monarch caterpillars.

Physiological Ecology and the Annual Cycle: four papers examining hormonal control of reproductive diapause and thermal biology during overwintering in monarchs and other danaid species.

Migration: eight papers, including several which challenge the conventional wisdom about the migration phenomenon.

Overwintering Biology: eight papers covering the distribution and ecology of Californian and Mexican overwintering sites, and various aspects of predation ecology in the Mexican colonies.

Conservation: one long paper and seven brief reports on aspects of the monarch conservation efforts in Mexico and California.

Unfortunately, there is no cumulative bibliography at the end. This makes the reproduction of individual articles easier, but hampers a quick but comprehensive survey of the breadth of the literature. Printing individual citations also must have added substantially to the length of the book: some references are cited repeatedly (e.g., Urquhart, 1960, 15 times; Tuskes and Brower, 1978, 11 times; Brower, 1984, 12 times).

Several contributions in the book deserve individual praise. Van Hook's revelation that small, tattered males preferentially mate with large females in good condition at the annual breakup of Mexican overwintering colonies in March illustrates the complex behavioral tradeoffs which surround reproduction and remigration. Malcolm, Cockrell and Brower's elegant study of cardenolide fingerprints conclusively demonstrates the stepwise recolonization of North America by successive broods. Snook presents a detailed and realistic analysis of factors impinging upon monarch conservation at the Mexican overwintering sites, from mistletoe infestations to the poverty of the local people.

The major flaw of this volume is its tardiness in reaching the market. The conference was held more than six years prior to the publication date. It is evident from their failure to accommodate relevant recent publications that many of the manuscripts have not been revised since the late 1980's. Thus, a number of papers have been
anticipated or superseded by publications already available in the periodical literature. In particular, Ritland and Brower's paper on monarch-viceroy (Limenitis archippus) mimicry is a recap of Ritland and Brower, 1991 and Ritland, 1991; VaneWright's Columbus Hypothesis has largely been covered by a lively debate in Antenna (Vane-Wright, 1986, 1987; Malcolm and Brower, 1987) and Malcolm's discussion of the overwintering colonies as an endangered phenomenon has appeared in some form at least twice before (Brower and Malcolm, 1989, 1991).
The datedness of the material is perhaps most evident in the papers that focus on conservation. Aside from Snook's excellent study, most of the contributions are short reports on then-current conservation activities in Mexico, by Monarca A. C, and in California, by the Monarch Project of the Xerces Society. At the time of the conference, then President Miguel de la Madrid had just declared four of the Mexican overwintering sites as ecological reserves, and there was a strong sense of optimism over conservation prospects for those sites. Since 1986, however, one of the sites has been clear cut, and governmentally sanctioned logging proceeds adjacent to the others. Lumber and firewood harvesting by area residents also continues to diminish habitat size, quality and sustainability.
In sum, this book is a collection of generally high-quality studies on various aspects of monarch biology. It will endure more as a source for particular articles than as a comprehensive reference on monarch biology, because it provides but a series of aging snapshots in the vast panorama of our knowledge about the species.-Andrew V. Z. Brower, Dept. of Entomology, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024-5192.

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Butterflies through Binoculars, A Field Guide to Butterflies in the Boston, New York, Washington Region. - Jeffrey Glassberg. 1993. Oxford University Press, New York, x +160 pp., 40 color plates and facing legends. Available in both hardcover (ISBN 0-19-507982-5) and softcover (ISBN 0-19-507983-3).

Butterfly watching, or "butterflying" as the author of this small innovative book refers to it, has constantly gained adherents and currency since 1974 with the publication of Robert Michael Pyle's "Watching Washington Butterflies," a photographic field guide to the butterflies of Washington State. Roger Tory Peterson has stated that butterflying is at the same stage that birding was when his first field guides appeared. A great increase in the popularity of butterflying is anticipated over the coming decades. This book will have been one of the contributing factors.

Most recent butterfly guides have devoted some or even most of their attention to butterfly watchers and photographers but none has done so as completely as the book under review. Jeffrey Glassberg's well written and accurate book on butterflies of the "Bos-Wash" urban corridor brings in some new firsts. On the inside covers are black silhouettes of representive butterflies from the seven families covered. Scientific names with authors are given with the species accounts but only common names are mentioned elsewhere in the text. Identification characters are more or less limited to those than can be observed in the field. A number of characters usable in the field, but not mentioned in earlier treatments, were developed by Dr. Glassberg and fellow members of the New York Butterfly Club.

The coverage of species is virtually complete; I am aware of only a few vagrant species that were omitted. These include the Early Hairstreak (Erora laeta), Acmon Blue (Plebejus acmon), and the Northern Pearl Crescent (Phycoides selenis).

The species accounts are tight and well organized; only the overuse of initializations mars their usefulness. Each account includes size (given relative to some common butterfly), identification, habitat, range (including total range), flight period and abundance (including known dates for each of the major urban areas), major foodplant, and comments.

The color plates, with one exception, are comprised of color photos of butterflies taken in nature. Most are good to excellent photos, but a few are blurry. These photos when accompanied by the text will allow the observer to identify almost all of the butterflies in the area covered. Unfortunately, a few photos are misidentified: Plate 17, Figure 4 is the Green Comma (Polygonia faunus), not Polygonia progne and Plate 22, Figure 3 is the Appalachian Brown (Satyrodes appalachia), not Satyrodes eurydice. Plate 28, Figure 3 is a photo of a female of the Pyrgus communis complex taken in the Lower Rio Grande Valley of south Texas and is not identifiable to species, since genitalic examination or presence or absence of a costal fold are needed to identify the three members of the complex found in that area.

There are several useful appendices following the species accounts. These include a guide to butterfly sites in the area covered by the guide, dates of appearance of New York area butterflies, phenograms for New York area butterflies, a checklist of butterflies treated, a listing of butterfly clubs and societies, butterfly count areas and contacts, a glossary, and list of references.

I recommend this book for the libraries and field sacks of all readers who live in
the area covered. The usefulness of the book declines as one travels away from the coverage area. Elsewhere in the eastern U.S. other books such as the recent Peterson Field Guide should be referenced.-Dr. Paul A. Opler, National Biological Survey, 1201 Oak Ridge Drive, Suite 200, Fort Collins, Colorado 80525.
J. New York Entomol. Soc. 102(3):401-403, 1994

A Functional Biology of Parasitism: Ecological and Evolutionary Implications.-G. W. Esch and J. C. Fernandez. Chapman and Hall, Cambridge, 1993. ISBN 0412 39910 5; 337 pp., 81 figs.

There has been a steadily growing interest in the role of parasites in ecological and evolutionary studies during the latter half of this century. This interest has been encouraged by the search for rigorous approaches to the issues of historical associations (coevolution) of hosts and parasites and the related historical ecology, microevolutionary arms race scenarios between hosts and parasites, the relationships between parasites and sexual selection of their hosts, the Red-Queen hypothesis, and the ecological constraints surrounding parasite and host community structures. Parasites have become so compelling as research subjects, in fact, that "A Functional Biology of Parasitism" by Esch and Fernandez will be found on book store shelves alongside, and in competition with, other recent works such as "Phylogeny, Ecology and Behaviour" and the just released "Parascript" both by Brooks and McLennan as well as "Natural Enemies" by Crawley and "Bird-Parasite Interactions" by Loye and Zuk. The strengths of "A Functional Biology of Parasitism" are primarily in the field of host-parasite community structure and dynamics. Those interested in phylogenetic or biogeographical aspects of parasite biology should, however, look elsewhere as these are dealt with in only a cursory way by Esch and Fernandez.

The Introduction may well dissuade many from going on and reading the rest of the book as it jumps straight into helminthology, moving from one specific example to the next rather than priming the reader with a few generalizations about parasite biology. This is unfortunate as it does a disservice to the contents that follow. Little is given up by moving quickly to the second chapter, Population Concepts, and perhaps reading the last chapter, the Summary, before deciding whether to proceed. The most valuable contribution made by the authors is that chapters 3 through 7 serve as an unrivaled compilation of case studies of helminth parasite population biology and a valid attempt to summarize elements of modern ecological theory within a parasitological framework. Moreover, the perspectives of infra-, meta-, and suprapopulations are maintained throughout, not only in the text but in the graphical representations of life cycles. Some factors that play fundamental roles in the lifehistories and transmission dynamics of helminths are addressed (Chapter 3), as are factors involved in host population structure (Chapter 4). With respect to the latter, the authors provide a useful digression into the origins of modern methodology with Crofton's early approaches to parasite regulation of host populations leading into the more realistic approaches of May and well-designed investigations by Scott. Unfortunately, the naive reader might be left with the expectation that parasites are known
to regulate host populations as opposed to being made aware that this remains a hotly debated notion. The section on modeling, though brief, is among the more enlightening and should serve as an inducement to parasitologists to construct testable hypotheses and appropriate experimental designs. Chapter 5 (Life History Strategies) makes for very interesting reading, providing a flavour for the variety of modes of transmission among parasitic helminths and how this relates to multiple stages in life-histories, host-seeking behaviours, morphology, reproductive strategies and selection regimes. Chapters 6 and 7 (Infracommunity Dynamics, and Component \& Compound Communities, respectively) are related and should be read as though they were a single chapter dealing with the ebb and flow of parasites among the members of host populations at various levels of the life cycle. The study of the dynamics of parasite flow through ecosystems and food webs, near the end of Chapter 7 , highlights an exciting research programme that is still largely untapped. In these chapters as in the next (Biogeographical Considerations) the authors seek to explain the distribution of parasites among hosts primarily in terms of colonization and local extinction, relegating the role of historical macroevolutionary constraints to an ancillary position. Similarly, in Chapter 8 (Evolutionary Aspects) they provide a concise overview of recent microevolutionary lines of investigation such as genetic variability, gene tracking between hosts and parasites, the Red-Queen hypothesis and sexual selection studies. The authors treat issues of phylogenetic relationships, however, only briefly and conclude that phylogenetic systematics is unreliable, citing as evidence a fantastical mechanism in which retroviruses transfer genetic material between hosts and parasites.

The authors endeavor to define carefully all components of parasite ecology, some repeatedly as is necessary, allowing ease of understanding for the ecological novice. The book suffers, however, from an emphasis on helminthological parasites, alimentary ones in particular. This leads the authors to accept such conclusions as amphibians and reptiles are "the least diverse and most depauperate of the vertebrate groups" with respect to parasites that inhabit them. This may be true for intestinal helminths, but when metazoan parasites of viscera and muscle of frogs are considered the perspective changes markedly. Moreover, when one adds protozoan parasites of the blood and intestines of anurans, the parasitic fauna becomes enormous. The reliance on intestinal helminthology stems more from the available ecological studies than from the authors' bias. In fact, they repeatedly conclude the subsections of each chapter with cautions, emphasizing how difficult it is to draw conclusions on the basis of such limited data. In addition to the authors' urgent calls for more longterm studies, a shift toward appropriate experimental design should be added.

This book will be of greatest value at the student level and to traditional parasitologists (helminthologist and protozoologist alike) who have had limited exposure to, or interest in, studying the population biology and ecological interactions that pervade the lives of their parasites of interest. In reading "A Functional Biology of Parasitism," one quickly sees the lines of investigation that have been followed fruitfully as well as the pitfalls that await. By far the work most cited is that of Esch and his collaborators (including Aho, Bush, Holmes and Kennedy). Non-traditional parasitologists such as entomologists will undoubtedly be disappointed in the absence of examples or reference to the extensive ecological literature on gall-forming midges or wasps, inquilines and parasitic wasps and flies. Some attention is given to the
important role played by arthropods as intermediate hosts of helminths and a quick look at the Taxonomic Host Index will point to these. Those who are interested generally in ecology and population biology will find interesting examples of applications from among the community of helminthologists and the distinctiveness of some of the questions, but may find some of the data analysis less than compelling or entirely up to date. A chapter on experimental design and statistical evaluation of ecological data is noticeably lacking from this book and would have added significantly to its value. As it is, "A Functional Biology of Parasitism" is best seen as a reasonably thorough compendium rather than a how-to book on parasite population biology.-Mark E. Siddall, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

## INSTRUCTIONS TO AUTHORS

The Journal of the New York Entomological Society publishes original research resulting from the study of insects and related taxa. Research that contributes information on taxonomy, classification, phylogeny, biogeography, behavior, natural history, or related fields will be considered for publication. 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.

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## Journal of the New York Entomological Society

## CONTENTS

Absence of kin discrimination behavior in a soldier-producing aphid, Ceratova- cuna japonica (Hemiptera: Pemphigidae; Cerataphidini)
Norman F. Carlin, David S. Gladstein, Andrew J. Berry, and Naomi E. Pierce ..... 287-298
Cladistic placement of the Subantarctic genus Haversiella (Coleoptera: Cur- culionidae) Juan J. Morrone ..... 299-302
Fossil Cydnidae (Heteroptera) in the Dominican amber Donald B. Thomas
303-309
A new case of parthenogenesis in beetles: Longitarsus melanurus (Melsheimer) (Coleoptera: Chrysomelidae) David G. Furth ..... 310-317
A revision of the genus Thasus (Hemiptera: Coreidae: Coreinae: Nematopodini) Harry Brailovsky, Carl W. Schaefer, Ernesto Barrera and Richard J. Packauskas ..... 318-343
Etapocanga, a new genus and two new species of neotropical flea beetle (Coleoptera: Chrysomelidae: Alticinae) Catherine N. Duckett ..... 344-349
Description of the larva of an unidentified species of Ceratopuis Schoenherr, with comments on plant associations in Ceratopodinae (Coleoptera: Curculionidae) James Pakaluk and Tami A. Carlow ..... 350-354
A remarkable new bamboo lygaeid from Mexico and a new species of Patritius from Venezuela (Hemiptera: Lygaeidae: Blissinae)
James A. Slater and Harry Brailovsky ..... 355-360
A description of the immature stages of Paduniella nearctica (Trichoptera: Psy- chomyiidae) with notes on its biology Michael L. Mathis and David E. Bowles ..... 361-366
A new species of Leotichius from Bali, with notes on immature stages and habitat (Heteroptera, Leptopodidae) John T. Polhemus and Randall T. Schuh ..... 367-373
Two new species of Atractotomus from southern Mexico (Heteroptera: Miridae: Phylinae) Gary M. Stonedahl and Michael D. Schwartz ..... 374-380
Notes and Comments
Neotype designation for Ranatra americana edentula Montandon (Heteroptera: Nepidae) John T. Polhemus ..... 381-383
Predation by Clivinema coalinga Bliven (Heteroptera: Miridae: Deraeocorinae: Clivinemini) of Orthezia annae Cockerell (Sternorrhyncha: Ortheziidae) Richard S. Miller and Randall T. Schuh ..... 383-384
Megatoma (Pseudohadrotoma) kaliki (Coleoptera: Dermestidae): Range exten- sion and character variation R. S. Beal, Jr. ..... 384-385
A southern distribution for the introduced dung beetle Aphodius (Otophorus) haemorrhoidalis (L., 1758) Jorge M. Lobo ..... 385-386
Book Reviews
Behaviour and Social Evolution of Wasps: The Communal Aggregation Hypoth- esis James M. Carpenter387-3.89
The Insects of Macau Richard G. Robbins389-391
Proceedings of the Second International Congress of Dipterology Rudolf Meier ..... 391-394
Nymphs of North American Stonefly Genera (Plecoptera) Sule Oygur ..... 394-396
Verzeichnis der Sandlaufkäfer der Welt (Coleoptera, Cicindelidae)Sanford Leffler396-397
Biology and Conservation of the Monarch Butterfly Andrew V. Z. Brower ..... 397-399
Butterflies through Binoculars, A Field Guide to Butterflies in the Boston, New York, Washington Region Paul A. Opler ..... 400-401
A Functional Biology of Parasitism: Ecological and Evolutionary Implications
Mark E. Siddall401-403

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# NATURAL HISTORY OF LEAF-FOLDING GATERPTHEARSA DICHOMERIS SPP. (GELECHIIDAE), ON GOLDENRODS AND ASTERS AUG U 31995 <br> Carol C. Loeffler* 

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Abstract. - Ten species of caterpillars in the genus Dtthomeris were collected on Solidago and Aster spp. in the northeastern U.S.; an eleventh species was collected on Solidago in Florida. New host records are presented. Most species fly in summer and overwinter as partly grown larvae. Some species are restricted to open habitats; others occur in both forest and field. Larvae can be distinguished by color pattern. All but one of the species are leaf folders; some species fold leaves tightly and others loosely. Overall forms of leaf folds vary among host plant species, reflecting differences in position of natural bends in the leaves which larvae always choose as starting points for leaf folds. Ovipositing adults D. leuconotella and D. ochripalpella prefer tall ramets, so that eggs and summer-hatching larvae are concentrated on the tallest host plant species (S. altissima). Partly grown caterpillars redistribute themselves more evenly among host species in the following spring. Adults of at least four species avoid ovipositing on S. caesia, although $S$. caesia is much used by the single apparently spring-hatching species, D. bilobella. Parasitoids are shared among the summer-hatching caterpillar species; D. bilobella is attacked by a different set of parasitoids.

Caterpillars in the large genus Dichomeris (Gelechiidae) often feed on composites, particularly Solidago and Aster species. Hodges (1986) listed 12 North American Dichomeris species that had been reared from Solidago and/or Aster species, ten of which occur in the northeastern United States. In New York State, Dichomeris is by far the most diverse of the lepidopteran genera recorded on Solidago (Forbes, 1923, 1948, 1954, 1960; R. B. Root, C. C. Loeffler, and J. E. Rawlins, unpubl.). The caterpillars of most of the species are leaf folders.

This paper presents data from six years of collections, rearings, and behavioral observations of Dichomeris species, primarily on Solidago spp. but also on the closely related species Euthamia graminifolia (L.) and on Aster spp. Included are many new or more specific host plants records as well as records of two Dichomeris species whose caterpillars were previously unknown. Also included are data on relative abundances, habitat distributions, phenology, and behavior of the various species' caterpillars, as well as notes on adult biology and behavior and on identities and relative abundances of the species' parasitoids.

## METHODS

Field collections, rearings, and identifications. From 1983 to 1988, I collected and reared Dichomeris caterpillars from goldenrods and asters in a variety of habitats

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Fig. 1. Locations of collections of Dichomeris species: 1. Essex County, New York: several fields, forest openings, and forests. July-August, 1983-1991. 2. Tompkins, Tioga, Cayuga, Seneca, Schuyler, and Cortland Counties, New York: Forty-three sites, in a variety of habitats as shown in the local map in Figure 2. Mostly in April-October, 1983-1988. 3. Hampshire County, Massachusetts: several sites along forest edges and in roadside fields. Late April, 1985 and 1988.4. Orange and Broome Counties, New York, and Lackawanna and Luzerne Counties, Pennsylvania: fields along Interstates 84 and 81. Late April-May or June, 1983-1988. 5. Berks, Lehigh, Carbon, and Schuylkill Counties, Pennsylvania. Several large fields, forests, and fields succeeding to forest. April-Oct, 1983-1984 and early May, 1985. 6. Leon County, Florida: large fields, Tall Timbers Research Station, Tallahassee. April 1984. 7. Highlands County, Florida. Open scrub, Archbold Biological Station, Lake Placid. March-April 1984.
and geographic locations (Figs. 1, 2). In 1983, to establish caterpillar species presences in oldfields, I examined 15-25 ramets each of the five most abundant field goldenrod species, Solidago altissima L., S. rugosa Ait., S. juncea Ait., S. gigantea Ait., and Euthamia graminifolia, in four fields in areas a, b, and c of Figure 2 (Cayuga Lake Basin of Central New York). During these samples, conducted every 1-2 weeks from late May to mid September, I searched all aboveground portions of each ramet and collected all caterpillars on the ramets for rearing and identification.

In 1984, seeking comparative data for forests and fields, I took regular samples of 50 ramets each of $S$. altissima and $S$. rugosa in an oldfield and 50 ramets each of $S$. rugosa and S. caesia L. in adjacent upland forest in area c of Figure 2. I took similar sample in an oldfield and an adjacent swampy forest in area b (Fig. 2), but I substituted Aster lateriflorus L. for $S$. caesia which was scarcer at that locality. I took these samples at 10-15 day intervals from early May to late September.

Additional, informal collections were taken from any species of goldenrod or aster encountered in the various sites in Figures 1 and 2. Some larvae were collected during annual June and September surveys of the fauna of S. altissima in 22 oldfield sites scattered throughout the Cayuga Lake Basin. (Data from these surveys are presented in Root and Cappuccino, 1992.) I took large spring collections from fields and forests in areas a-e (Fig. 2), which supplied most of the captive breeding stock. Finally,


Fig. 2. Locations of the 43 sampling sites in the Cayuga Lake Basin and surrounding area of central New York. Lettered circles represent intensely sampled areas, as indicated in Methods. Closed circles represent oldfield sites sampled in June and September. Open circles represent irregularly-sampled forests, forest edges, streambanks, gravel bars, or beaver meadows.
smaller collections were made at various times from April to October in natural or semi-natural forest openings (small clearings, beaver meadows, streambanks, and gravel bars) and in additional forest and field sites. Some sites were visited specifically because they harbored an unusual goldenrod or aster species.

Gravel bars were of special interest because they may have been strongholds of "field" goldenrod species before European settlement (Marks, 1983), yet they may be inhospitable sites for most Dichomeris species whose caterpillars overwinter in the ground litter. To determine whether overwintering was possible in such sites, I augmented natural populations of young larvae on two gravel bars in October, 1984 (for details of methods used see Loeffler, 1992). I revisited the bars to collect surviving larvae in May, 1985.
Rearing methods are described in Loeffler (1992). Briefly, caterpillars were generally reared individually in glass scintillation vials or in small groups in plastic boxes, on excised leaves of S. altissima or other available host species. Rearings in 1985 occurred outdoors, in an open barn. Also, over four hundred caterpillars, mostly of $D$. leuconotella (Busck) and D. bilobella (Zeller), were monitored on live plants in field or forest, often in cages (dacron sleeves tied over the plants). Phenological information in this paper is based on field observations and outdoor rearings.

Dichomeris adults were identified by R. W. Hodges, J. E. Rawlins, and me. Parasitoids were identified by J. E. O'Hara (tachinids) and by the following research entomologists at the U.S. National Museum: P. M. Marsh (Braconidae), M. E. Schauff
(Eulophidae, Encyrtidae), and R. W. Carlson (Ichneumonidae). Voucher specimens are deposited in the U.S.N.M. and in the Cornell University Insect Collection under Lot No. 1209.
Observations and manipulations to examine larval biologies. I followed several hundred Dichomeris larvae of the different species through part or all of their development, on a variety of Solidago and Aster species. Captive breeding colonies allowed study of newly hatched larvae of several species. To study the life history of $D$. bilobella, whose young larvae were curiously absent in the field when those of other species were appearing in late summer, required a different protocol. I caged many D. bilobella adults on several species of goldenrods and asters in summer and examined the potted plants for larvae through late summer and autumn. I then covered the pots and their senesced ramets with muslin and overwintered them outdoors, keeping the soil in the pots slightly moist. In spring I monitored the new ramets for larvae.

Overwintering biology of summer-hatching species was studied in several ways. I reared larvae of several species indoors to determine requirements for winter dormancy. To follow larval movements to and from winter refuges, I took Tulgren funnel extractions of leaf litter from the ground and from standing ramets, at various times in fall and spring. I also monitored captive individuals overwintered outdoors in containers of leaf litter, and I observed their behavior on emergence from overwintering refuges in spring. One set of trials addressed how far larvae wander from their autumnal host: I introduced early instar D. flavocostella (Clemens) and D. leuconotella larvae (about 45 of each species) to clumps of S. altissima ramets growing outdoors in the center of four $60 \times 60 \mathrm{~cm}$ wooden boxes in October 1984 and trapped them from surrounding leaf litter in the following spring before new $S$. altissima ramets began to appear aboveground. Trapping was accomplished by collecting leaf litter from various zones in the boxes $-0.5 \mathrm{~cm}, 5-30 \mathrm{~cm}$, and $>30 \mathrm{~cm}$ from the dead plant ramets-and placing the leaf litter from each zone in a separate large dishpan indoors in which there already grew many new S. altissima ramets. I examined these plants every day or two thereafter for larvae emerging from the litter.
Adult behavior and host plant preference. I bred adult moths in insect cages or in large plastic rearing boxes. Water and either cut fruit or a solution of honey and water was provided every 1-2 days (the liquids via soaked paper tissues). For oviposition, I added cut host plant ramets (with their bases in vials or jars of water) or potted host plants. I made informal observations of the moths' feeding and mating behavior at various times of day and night.

To study adult host plant choice in D. leuconotella, D. flavocostella, D. ochripalpella (Zeller), and D. levisella (Fyles), I set up cages each containing one 15 cm ramet top of $S$. rugosa collected in oldfield, one 15 cm ramet top of $S$. rugosa collected in forest, and two 25 cm ramet tops of the strictly forest species $S$. caesia. I presented an excess of $S$. caesia as a conservative measure, because 1984 observations using potted plants suggested that it was not favored as a host. I placed ramet tops in uniform-sized jars of water, inserted through a perforation in the lid, and caged several male and female moths with each group of plants for four-five days. Numbers of eggs laid on the three types of goldenrods were compared with a Quade test (Conover, 1980), or with a G test (using Williams' correction, Sokal and Rohlf, 1981) for species with four or fewer trials. G tests required the assumption that each egg represented independent laying
events, which was probably generally the case; but egg distributions suggested that moths occasionally "dribbled" two or more eggs in rapid succession.

Similar oviposition trials addressed why young, later summer Dichomeris larvae are more numerous on $S$. altissima than on the other common field species, $S$. rugosa (Fig. 9). Preference for $S$. altissima could result simply from its greater height. To test this possibility, I set up cages each with tall $(28 \mathrm{~cm})$ and short ( 14 cm ) ramet tops of $S$. altissima and $S$. rugosa arranged in a Latin square design (16 ramets per cage). Numbers of eggs laid over several days were analyzed using a Quade test ( $D$. leuconotella, 12 trials) or a goodness of fit $G$ test (D. ochripalpella, four trials).

## RESULTS

Distributions, relative abundance, and host plants. I collected 11 species of Dichomeris from Solidago spp., Euthamia graminifolia, and Aster spp.: 10 in the Northeast and two of these plus an additional species in Florida (Table 1, Fig. 1). The 11 species included nine previously reared by lepidopterists from Solidago and/or Aster, and two ( $D$. purpureofusca and $D$. achne) whose caterpillars were previously unknown (Hodges, 1986). Three other North American Dichomeris species have been reared from these host genera by previous workers. One of these, D. copa Hodges, occurs in the northeastern U.S. and Canada; the only rearing record was from Solidago in Nova Scotia (Hodges, 1986). Its absence from my collections implied local rarity, at least on Solidago. The other two are a western species and a species known only from Kentucky (Hodges, 1986).

Five of the species were sufficiently common that I was able to document habitat distribution patterns. Dichomeris bilobella was most numerous in forests, reaching high densities ( $10-50 \%$ of ramets damaged) for several years in succession in certain hillside woods characterized by abundant $S$. caesia and other hosts. Such densities are exceptional for goldenrod- and aster-feeding Dichomeris: spring populations of all species combined in large fields rarely averaged more than one larva per 10 ramets (Root and Cappuccino, 1992). Dichomeris bilobella also was abundant spottily along some field margins, but it was rare in large fields.

The most common species in large and contiguous fields were $D$. flavocostella in eastern Pennsylvania and Florida, and D. leuconotella from northern Pennsylvania northward. With rare exceptions, I found neither of these species in forests or small forest openings; nor did R. A. Hamilton, who sampled forest and field goldenrods extensively in central New York during the same years (1989 and pers. commun.).

A fourth species, D. levisella, occurred fairly consistently in isolated forest openings as well as fields, but never within the forest proper. Balduf (1969) collected large numbers of $D$. levisella in northeastern Minnesota on Aster macrophyllus, which he reported as favoring "open places on high ground, such as clearings and roadways through woodlands."

A fifth species, D. ochripalpella, was evenly distributed among forest and large or small field habitats; except that it was extremely rare on the common forest goldenrod $S$. caesia, and hence was restricted to areas containing other host species.

The remaining six species were collected in open habitats. Among them, D. nonstrigella showed great regional variation in abundance: large populations inhabited certain Massachusetts and Pennsylvania fields and roadsides (areas 3 and 4c of Fig.
Table 1. Dichomeris species collected at localities in Figures 1 and 2. Sampling efforts concentrated on Solidago species, especially S. altissima, S. rugosa, and S. caesia. Records are based on my rearings of caterpillars to adulthood except in the following cases: 'Records based on larval identifications; collected caterpillars failed to reach adulthood. (Question marks in the table reflect probable but not certain larval identifications.) ${ }^{2}$ Records based on collections and rearings to adulthood by R. H. Hamilton (1989 and pers. comm.), who sampled insects extensively on $S$. altissima, S. rugosa, S. bicolor L., S. flexicaulis L., and E. graminifolia. ${ }^{3}$ Collected as pupa in leaf fold; no other likely hosts nearby.

Host plants

| Common species |  |  |  |
| :---: | :---: | :---: | :---: |
| 1. Dichomeris bilobella (Zeller) | 1,2,3, 4, 5 | large and small fields, isolated forest openings, and forests | Solidago altissima, S. arguta, Ait., S. bicolor ${ }^{1.2}$, S. caesia, S. canadensis L. ', S. flexicaulis, S. gigantea, S. juncea, S. nemoralis Ait., S. rugosa, Aster cordifolius L., A. divaricatus L., A. lateriflorus, A. macrophyllus L., A. lanceolatus Willd., A. undulatus L. |
| 2. D. flavocostella (Clemens) | 1?, 2, 3, 4?, 5, 6 | large or contiguous fields | S. altissima, S. arguta, S. bicolor $^{2}, S$. juncea? ${ }^{1}$, S. rugosa, A. novae-angliae L., A. lanceolatus |
| 3. D. leuconotella (Busck) | 1,2,3, 4, 5 | large or contiguous fields | S. altissima, S. bicolor?', S. caesia ${ }^{2}$, S. gigantea, S. juncea, S. rugosa, Euthamia graminifolia, A. novae-angliae ${ }^{1}, A$. sagittifolius Wedemeyer |
| 4. D. levisella (Fyles) | 1 ?, $2,3,4,5$ ? | large and small fields including isolated openings in forests | S. altissima, S. gigantea ${ }^{1}$, S. rugosa, E. graminifolia ${ }^{1}$, $A$. lanceolatus ${ }^{1}$ |
| 5. D. ochripalpella (Zeller) | 1,2,3, 4, 5 | large and small fields, isolated forest openings, and forests | S. altissima, S. bicolor ${ }^{2}$, S. caesia ${ }^{2}$, S. flexicaulis ${ }^{2}$, S. gigantea, S. juncea', S. patula Muhl., S. rugosa, E. graminifolia ${ }^{1.2}$, A. cordifolius ${ }^{1}$, A. divaricatus, , lateriflorus, A. novae-angliae, A. prenanthoides Muhl, A. sagittifolius, $A$. lanceolatus, $A$. undulatus |
| Rare species |  |  |  |
| 6. D. inserrata (Walsingham) | 2, 5, 6 | large fields | S. altissima |
| 7. D. nonstrigella (Chambers) | 2, 3, 4 | large field, roadside, small forest opening | S. altissima, S. gigantea, S. rugosa |

Table 1. Continued.

|  | Localities | Habitats | Host plants |
| :---: | :---: | :---: | :---: |
| 8. D. purpureofusca (Walsingham) | 1,2 | large fields, small opening near large fields | S. altissima |
| Species encountered only in one locality, not in central NY |  |  |  |
| 9. D. achne Hodges | 7 | on isolated patches of Solidago in open scrub | S. fistulosa Miller |
| 10. D. agonia Hodges | 5 | dry open roadside | S. juncea, S. nemoralis |
| 11. D. juncidella (Clemens) | 1 | large field | S. gigantea ${ }^{3}$ |

Table 2. Additional host records, from Hodges, 1986, for the Dichomeris spp. collected in this study. Records duplicating those in Table 1 are omitted except when the record in Table 1 was not based on rearings from larva to adulthood.

| Caterpillar species | Host plants |
| :--- | :--- |
| D. leuconotella | Solidago uliginosa Nuttall, Helianthus grosseserratus M. Martens |
| D. levisella | Aster macrophyllus, A. cordifolius, A. lanceolatus, Hieracium aurantia- |
|  | cium L. |
| D. nonstrigella | Aster shortii Lindley |
| D. ochripalpella | "composites" |
| D. agonia | Aster sp., Oenothera sp. |
| D. juncidella | Solidago sp., Aster sp., Ambrosia artemisiifolia L., Artemisia trifida L., |
|  | Helianthus tuberosus L., Aralia spinosa L., "strawberry" |

1), but I encountered only one individual in the Cayuga Lake Basin samples and none in other regions.

Gravel bars, a potentially important goldenrod habitat before forests were opened by man, were inhabited by all of the common summer-hatching species ( $D$. flavocostella, D. leuconotella, D. levisella, and D. ochripalpella). Early instar caterpillars overwintered successfully in fair numbers on the two bars to which I transplanted them in the fall of 1984, despite the sparseness of leaf litter. The latter two bars were however spared from floods and ice scouring that winter, leaving open the possibility that gravel bars might have to be recolonized by moths that developed on host plants well up on the streambank or in more distant areas after years of exceptionally harsh physical conditions.

Many of the host plant records in Table 1 are new. Additional host records from museum specimens and the literature are summarized in Table 2, including records of plants other than Solidago, Aster, and Euthamia. I found that larvae could be switched from one aster or goldenrod species to another; in particular, larvae collected on asters fed readily on goldenrod, and vice versa. [Controlled experiments might detect depressions in growth rate or survival on certain host species; for example, early instar $D$. leuconotella larvae had poor survival and growth on $S$. caesia (Loeffler, 1992).]

Phenology. In the Northeast, Dichomeris species showed three phenological patterns (Fig. 3). Moths of four of the five common species (D. flavocostella, D. leuconotella, D. levisella, and D. ochripalpella) eclosed in late June in central New York. Judging from laboratory matings, they laid eggs through July and possibly into August. The eggs, which were laid singly on leaf undersides, hatched in as little as six days into 1 mm long larvae. These larvae grew slowly to $3-4$ or occasionally 5 mm (second to fourth instars) before leaving the plants in October to overwinter in the leaf litter. By mid-November, larvae emerged in Tulgren funnels only from ground litter samples, not from equal-weight samples of leaves on standing ramets.

In late April or early May in central New York, shortly after the emergence of new ramets, the larvae crawled up the plants and resumed feeding. Further growth was rapid; final instars began appearing as early as late May in warm years, and pupae appeared by early to mid-June (Fig. 3). Pupal development lasted about two weeks. The peak of adult eclosion for all four species was in late June and early July.


Fig. 3. Phenology of leaf-folding Dichomeris species on Solidago in central New York.
Moths of two less common species, $D$. nonstrigella and $D$. purpureofusca, flew on average approximately three weeks earlier, in June (Fig. 3). The life cycle was otherwise similar to that of the four species discussed above, except that larvae overwintered in their penultimate instar, at $>6 \mathrm{~mm}$ in length as indicated by fall and spring collections. Final instars were found in early to mid-May. Dichomeris agonia, collected only in Pennsylvania, apparently follows a similar life cycle because larvae collected in early May were considerably larger than those of the first group of four species in the same locality.

Moths of D. bilobella appeared latest, in July (Fig. 3). In the field, I search extensively but did not find young larvae in fall, even in an abundant population at area e (Fig. 2). Only two larvae hatched on plants exposed to adults in the laboratory, from unknown egg locations (unlike the other species, captive D. bilobella did not oviposit on the undersides of leaves). In late April and early May, I found 2-3 mm larvae (probably second instars) in large numbers, both in the field and on laboratory oviposition plants overwintered outdoors. The D. bilobella larvae were considerably smaller at this time than were the larvae of other species. They reached their final instar by mid to late June.
Larvae descriptions and development. Final instar larvae of eight species can be distinguished by the following key and by Figure 4 (the remaining species are discussed below). Leaf-folding behavior is included because it is one of the most reliable diagnostic characters.

## KEY TO GOLDENROD-FEEDING DICHOMERIS LARVAE OF NEW YORK AND NEIGHBORING STATES

1a. Ground color dark chocolate brown; stripes brownish black; white spots on both meso- and metathorax; body slightly spindle-shaped, head capsule small; leaf folds loose (Fig. 7)
D. purpureofusca

1b. Ground color pale to dark green; stripes green or brown; other traits variable ....... 2
2a. Two mesothoracic and two metathoracic tubercles much enlarged, black; white spots on both meso- and metathorax; thorax brown. Seven stripes (the two lateroventral stripes are not visible in the dorsolateral view shown); stripes greenish-brown, broad, even; body slightly spindle-shaped, head capsule small; leaf folds loose (Fig. 7) ....

## D. nonstrigella

2b. No tubercles enlarged; mesothorax black; metathorax black with white patches on posterior third; abdomen stripeless or with five green or brown stripes; body relatively linear; leaf folds variable

3a. Abdomen pea green and stripeless, except for a dorsal dark-green line (apparently
reflecting the internal contents of the caterpillar rather than the distribution of pig
ment); tubercles easily seen; leaf folds loose (Fig. 7)

3b. Abdomen pale green (whitish in molting specimens), with darker, green or brown
stripes; other traits variable ..... 4
4a. Stripes medium dark greenish brown to dark brown; lateral stripes extend to tip of abdomen, forming a V ; tubercles generally difficult to see against stripes; leaf folds loose (Fig. 7) ..... 5
4b. Stripes light to medium green or brownish green (light brown in molting specimens); other traits variable ..... 6
5a. Stripes medium dark greenish brown, broad, and even; anal V near-black and excep- tionally broad; largest species (up to 18 mm ) D. flavocostella
5b. Stripes dark watery brown; dorsal stripe usually narrow and faded, particularly atanterior end; anal V of same shade as stripes, less broad than in D. flavocostella (Note:some individuals overlap in characteristics with $D$. flavocostella and cannot be reliablydistinguished until they reach adulthood) . . . . . . . . . . . . . . . . . . . . . . . . . . D. leuconotella
6a. Lateral stripes greenish, not darkened on metathorax; lateral stripes extend only tomiddle of terminal abdominal segment; tubercles easily seen; smallest species (larvaup to 15 mm ); leaf folds tight (Fig. 7)D. ochripalpella
6b. Lower portions of lateral stripes nearly black on metathorax; other traits variable ..... 7
7a. Anal V dark brown; stripes pea-green; tubercles easily seen, surrounded by pale green rings; leaf folds tight (Fig. 7) D. bilobella
7b. Anal V medium green and obscure; stripes medium green, slightly lighter than thoseof $D$. bilobella; tubercles blend with stripes and are difficult to see; leaf folds loose(Fig. 7)D. levisella

Among the remaining three species collected in this study, larvae of $D$. inserrata lack stripes altogether and, unlike the other species, inhabit the terminal bud throughout their development rather than folded leaves. They are light green with relatively round black heads and thoracic shields. I have not seen larvae of D. juncidella; a description by Murtfeldt (1874) (as Depressaria dubitella) suggested that they are similar in overall pattern to $D$. bilobella and D. ochripalpella. The larvae of $D$. achne that I examined in south-central Florida closely resembled those of $D$. ochripalpella.

Lengths of full-grown larvae differed among the species, being approximately $16-18 \mathrm{~mm}$ for D. flavocostella, 15-17 mm for D. bilobella, D. leuconotella, and D. levisella, and 13.5-15.5 mm for D. ochripalpella, D. nonstrigella, and D. purpureofusca.

Larvae of $D$. leuconotella, the species that I monitored most closely, appeared to go through six instars when reared indoors. Also, preserved specimens sorted into six classes of head capsule size. But observations of newly emerged individuals in spring, thought to be third instars, suggested that some individuals pass through an extra molt with relatively little change in head capsule width while at overwintering size ( $3-5 \mathrm{~mm}$ ). Thus, some proportion of the population may pass through seven instars. Molts tended to occur at body lengths of $1.5-2.0 \mathrm{~mm}, 2.5-3.0$ $\mathrm{mm}, 3.5-4.5 \mathrm{~mm}, 6-7 \mathrm{~mm}$, and $10-12 \mathrm{~mm}$. Caterpillars of the other Dichomeris species also typically molted at these lengths.

Early-instar larvae are not easily identified to species. Among the species I bred (all those in Fig. 4 except D. agonia), first instars are $1-2 \mathrm{~mm}$ long and pale green with yellow heads and shields that darken through brown to black by the third instar, with some variation among species in rate of darkening. All develop stripes on the mesothorax in the late second or third instar; abdominal stripes appear and gradually darken during the third instar (or the fifth in $D$. bilobella). Dichomeris nonstrigella and D. purpureofusca caterpillars are distinguished from the third instar onward by an extra row of white spots on the metathorax, which are distinctive for each species (Fig. 4). The characteristic thoracic spikes of $D$. nonstrigella develop at variable rates over the third through fifth instars, and D. purpureofusca larvae gradually darken from green to nearly black over those same stages. Subtle differences distinguishing third, fourth, and fifth instars of the four common summer-hatching species (D. flavocostella, D. leuconotella, D. levisella, and D. ochripalpella) are described in Loeffler (1992); briefly, D. flavocostella stripes are uniform in width and the anal V becomes broad and dark during the third or fourth instar; D. leuconotella larvae have a narrow, faded or broken dorsal stripe and an anal V that is usually no darker and sometimes lighter than the rest of the stripes; and $D$. levisella stripes are relatively light in shade, except on the metathorax where the lateral stripes become dark brown. Third and fourth instar D. ochripalpella larvae are variable and intermediate among the other three species in all of these respects but are distinctive for the abrupt termination of all five stripes in the middle of the 10th abdominal segment, with only a thin shadow of an anal V continuing to the tip of the abdomen. The five stripes lighten to brownish-green or medium green (like those of $D$. levisella) after the molt to the fifth instar, at about $6-7 \mathrm{~mm}$.

Excellent keys, descriptions, and photographs of adults of the 11 species have been given by Hodges (1986). Live adult weights of some well-fed specimens corresponded well to the relative final lengths of larvae of the species, being $10-14 \mathrm{mg}$ for the large species D. flavocostella ( N $=4$ males, 5 females), $9-12 \mathrm{mg}$ for $D$. bilobella $(\mathrm{N}=6$ males, 2 females), $8-13 \mathrm{mg}$ for $D$. leuconotella ( $\mathrm{N}=5$ males, 3 females), $8-12 \mathrm{mg}$ for $D$. levisella ( $\mathrm{N}=5$ males, 2 females), and $5-10 \mathrm{mg}$ for the small species $D$. ochripalpella ( $\mathrm{N}=8$ males, 11 females).
Larval behavior. Newly hatched caterpillars were too small to fold leaves, and those of summerhatching species typically moved into whatever cracks or crannies were available near their hatch sites on the leaf undersides. Most larvae aligned themselves in the angle between a leaf midrib and the lower surface of the blade, although some moved into shelters created by other insects: between the clustered leaves of rosette galls (Rhopalomyia spp., Diptera: Cecidomyiidae) and button galls (Asphondylia sp., Diptera: Cecidomyiidae), inside the leaf mines of caterpillars of Cremastobombycia solidaginis (Lepidoptera: Gracillariidae), in leaf ties of other Lepidoptera such as Herpetogramma spp. (Pyralidae) and Phaneta formosana (Tortricidae), or even in old leaf folds of the previous generation of Dichomeris. The larvae spun a silk mat and rested beneath it, protected from predators by the silk and by their immobility (Loeffler, 1992). They fed in short bouts, creating small pits both beneath the mat and within a few millimeters of the opening at either end (Fig. 5a). Larvae of $D$. nonstrigella formed unusually long mats, virtual tunnels extending for many millimeters along the midribs and frequently branching to follow side veins (Fig. 5b). In all species, the addition of silk gradually caused the leaf to crinkle and fold over the mat (Fig. 5c), at a rate depending on the host species and the size and age of the leaf. Folded leaves provide a larger surface area for feeding within the protection of the refuge. Among caterpillars of the four common summer-hatching species (uppermost in Fig. 4), many


Fig. 4. Patterns and other diagnostic features of goldenrod-feeding Dichomeris caterpillars (dorsolateral views of final instars) in New York and neighboring states. For a key to final instars and for descriptions of younger larvae, see text. In all species, head capsules and prothoracic shields are black.


Fig. 5. Refuges of young leaf-folding Dichomeris larvae. a) Silk mat and feeding pits characteristic of most summer-hatching species. b) Longer silk tunnels characteristic of $D$. nonstrigella. c) Leaf cross sections showing how, by adding silk over a period of days or weeks, a caterpillar crinkles and eventually folds a leaf.
individuals remained in a single refuge for most of the late summer and fall; others left their refuges and constructed new ones several times over that period.

In October, caterpillars reared outdoors on excised leaves frequently left their refuges and crawled throughout the rearing vial, especially as the conditions of the leaves supplied to them deteriorated. Such wanderings presumably corresponded to the emigration of wild larvae from the senescing plants to the ground litter. These caterpillars eventually settled on senesced leaves and formed winter refuges consisting of short folds sealed at either end. The larvae formed similar sealed refuges in pieces of paper towel, when those were available. They remained in these shelters until spring. Although larvae generally ranged in length from 3 to 5 mm at this time, they were capable of overwintering at larger sizes; I successfully overwintered captive larvae outdoors at lengths of $3-9 \mathrm{~mm}$.

The slow development of young larvae in late summer was apparently enforced primarily by environmental factors and secondarily by genetic factors that varied among larvae. Young larvae reared at constant room temperature on fresh foliage responded differentially: some individuals of each species grew to adulthood without interruption while others grew extremely slowly or halted growth altogether for several months while in the $5-7 \mathrm{~mm}$ range. I maintained a continuously breeding indoor colony of $D$. leuconotella from summer of 1986 to summer of 1988, in which many individuals completed development from egg to adulthood in about three months.

In experiments addressing how far overwintering larvae strayed from their autumnal host, I found that some overwintering D. leuconotella and D. flavocostella larvae ( $3-5 \mathrm{~mm}$ in size) stayed within a few cm of their host and reascended it, or perhaps an immediate neighbor, in spring. Others however moved through the litter up to 30 cm or more between October and April. Thus, in diverse fields, larvae have opportunity to ascend hosts of different species than their fall ramets.

To study the caterpillars' behavior on a range of hosts of varied leaf morphology, I supplemented field observations with close monitoring of 14 field-reared D. leuconotella and D. levisella


Fig. 6. A representative sample of the refuges formed on different species of Solidago and Aster by early-to-middle-instar D. leuconotella and D. levisella larvae on spring rosettes. a) Exceptionally broad leaves such as those of Aster cordifolius were sometimes folded approximately transversely rather than lengthwise. b) On thin-leaved forest goldenrods ( $S$. caesia, $S$. arguta, S. flexicaulis), larvae typically first colonized the naturally upwardly-curled margin of a leaf that had not yet expanded from the terminal bud. Shown here are upper and lower sides of a leaf of $S$. caesia, with the larva's first refuge on the upper side, and with a later, larger fold constructed on the lower surface after the leaf had unfolded and assumed the downward flare characteristic of many leaves on these species. c) On leaves with downwardly bent auricles, as in the Aster novae-angliae leaf shown (viewed from below), or with strongly declinate wings running the length of the petioles as in A. novi-belgii or A. prenanthoides, the caterpillar formed a web and eventually a fold on the lower side, in the curl of the flange or wing. d) Narrow leaves of Euthamia graminifolia or A. pilosus were folded in half from the midrib, upward or downward depending on which way the leaves were naturally curved.
larvae on potted plants of 14 different species of Solidago, Euthamia, and Aster in early April of 1986. Larvae always sought out cracks or curves in the leaves that gave them a head start in constructing a refuge. Because the deepest cracks and curves varied in location among the host species, the larvae spun refuges that likewise varied in location and overall form depending on the nature of the host (Fig. 6, and see Loeffler, 1992).

Caterpillars made several refuges in spring, most of them during the final instar. Feeding damage began as pits, less that $1 \mathrm{~mm}^{2}$ in size, which did not puncture the leaf but left the opposite surface layer intact (Fig. 6). Feeding occurred several times per day, both in light and in dark (this was tested by examining plants immediately before and after placement in a closed cupboard at night). Each feeding bout lasted a few minutes. By the time the caterpillar was 67 mm in length and had molted to its penultimate instar, the pits were $1-2 \mathrm{~mm}$ wide and up to several mm long regardless of host species. Shortly thereafter, the larva typically began making indentations from the leaf margin, at either end of its refuge. Final instars ( $>10 \mathrm{~mm}$ )

## D. leuconotella

D. bilobella


6th instars


Fig. 7. Comparison of "loose" leaf folds of older caterpillars of D. leuconotella with "tight" leaf folds of $D$. bilobella (drawings copied from sketches of representative leaf folds). Other loose-folding species are D. flavocostella, D. levisella, D. nonstrigella, and D. purpureofusca; other tight-folding species are $D$. ochripalpella and D. achne.
sometimes still pitted the leaf, but they more typically chewed indentations in the margin, outside either end of the leaf fold. They also fed on adjacent leaves, which they reached by stretching between leaves or by actually wandering a cm or two up the stem. Refuges were abandoned as they became mangled, and new ones were typically built on higher leaves, so that the caterpillar stayed within the upper or upper-middle leaves of the plant as it grew. Regardless of host species, the larvae constructed a relatively narrow fold in which to pupate.
Larvae of $D$. bilobella, which did not appear until the spring following egg laying, had similar behavior to those of summer-hatching species except that early instars did not form mats on the undersides of leaves. Rather, they fed between leaves of the terminal bud, soon forming folds along the margins of terminal leaves expanding from the bud. Such behavior was possible because the leaves in the terminal buds of goldenrods and asters are large and pliable in spring; they are small or lacking by late summer.
Caterpillars of three species-D. bilobella, D. ochripalpella, and D. achne-characteristically folded leaves much more tightly than the others (Fig. 7). Their feeding damage consisted mainly of pits and indentations in the leaf margin outside either end of the fold (Fig. 8).
Adult behavior and host plant choice. Captive adults of the common goldenrod-feeding Dichomeris species were nocturnal: individuals that I monitored closely for 24 hours or more moved about chiefly after dark, and most of the times that I observed mating or feeding were at night.
The moths fed both on pieces of fruit and on dilute solutions of honey or boiled honey and fruit supplied in cotton or tissue. Although I rarely observed feeding, adult longevity (40-50 days or more for many individuals of both sexes) suggested that feeding is important. Egg production was much greater in small rearing boxes, where the moths were always in close proximity to food, than in large cages.


Fig. 8. Leaf-chewing damage of final instars of a) D. bilobella, a tight-folding species and b) D. leuconotella, a loose-folding species. Larvae of both tight- and loose-folding species frequently ventured one or two body-lengths from their refuges to chew on adjacent leaves. Goldenrod species shown are a) S. rugosa and b) S. gigantea.


Fig. 9. Results of 12 exposures of groups of $D$. leuconotella moths and 4 exposures of groups of D. ochripalpella moths to tall $(28 \mathrm{~cm})$ and short $(14 \mathrm{~cm})$ sprigs of two common field goldenrods. For $D$. leuconotella, differences in preference among the four types of sprigs were significant (Quade test, $\mathrm{T}_{1}=7.75, \mathrm{df}=3,33, P<0.01$ ), with followup comparisons indicating significant preference for tall ramets of either species over short ramets of either species, but no significant preference between $S$. altissima and $S$. rugosa. Results for $D$. ochripalpella were marginally nonsignificant (Quade Test, $\mathrm{T}_{1}=3.14, \mathrm{df}=3,9,0.05<P<0.10$ ), probably because of small sample size. If moths lay eggs singly rather than in close succession, then a goodness of fit $G$ test reveals highly significant results $(P<0.001)$ for $D$. ochripalpella.


Fig. 10. Number of Dichomeris caterpillars (combined species) per 50 stems of Solidago altissima or $S$. rugosa, averaged for two fields (areas b and c, Figure 2) sampled in 1984.

Females mated and began laying eggs within a week of eclosion. I usually kept moths in groups and did not attempt to quantify egg production per individual, but a $D$. purpureofusca female laid a total of more than 200 eggs over five weeks, and a D. flavocostella female laid 87 eggs over two days following three nights of mating activity. Production for most females was highest within the first two weeks following eclosion, although egg-laying generally continued throughout most of their adult lives.

Eggs of captive females were laid on upper, middle, and lower leaves and on stems, but typically on the lower surfaces of the leaves. Females of the two species tested, D. leuconotella and D. ochripalpella, showed a preference for taller ramets (Fig. 9). Such a preference has consequences for distribution of eggs among host species: S. altissima is the taller of the two common field goldenrods (Root, Loeffler, and Rawlins, unpubl.), and harbored a significantly greater abundance of late-summer larvae than did the shorter species $S$. rugosa in two fields in which these hosts grew intermingled (Fig. 10). In spring the larvae distribution on S. altissima and $S$. rugosa was more even (Fig. 10), presumably because the overwintered larvae encountered and ascended ramets indiscriminately.
Adults also had preferences among host species irrespective of size. Dichomeris leuconotella, D. ochripalpella, D. flavocostella, and D. levisella all laid more eggs on ramet tops of $S$. rugosa, especially field-grown plants, than on ramet tops of S. caesia (Fig. 11); although small numbers of trials (because of limited supplies of adults) constrained the statistical interpretations of the data for the latter two species (Fig. 11). Informal observations suggested that differences existed among several other host species as well, with S. altissima being perhaps the preferred host.
Parasitoids. Nineteen species of wasps in four families and one species of tachinid fly parasitized Dichomeris specimens in my collections, and three additional species of wasps occurred as hyperparasites (Table 3). Most of these parasitoids are polyphagous, attacking lepidopterous larvae or pupae of more than one family (Krombein et al., 1979). The frequent parasitoid Isomeris marginata may however specialize on Dichomeris; the only previous rearings were from Dichomeris levisella (as Pimplopterus marginata; Balduf, 1969). No other parasitoids in


Fig. 11. Results of exposures of groups of $D$. leuconotella (leuco, 15 trials), D. ochripalpella (ochri, eight trials), D. flavocostella (flavo, four trials), and D. levisella (levi, three trials) moths to sprigs of field and forest goldenrods. The first two species showed significant preference for $S$. rugosa, especially field-grown stems; the forest species $S$. caesia received almost no eggs. (Quade test for $D$. leuconotella: $\mathrm{T}_{1}=17.201$, $\mathrm{df}=2,28, P<0.01$; followup comparisons indicated significant preferences for field $S$. rugosa over forest $S$. rugosa and for forest $S$. rugosa over $S$. caesia. Quade Test for D. ochripalpella: $\mathrm{T}_{1}=20.577$, $\mathrm{df}=2,14, P<0.01$; followup comparisons indicated significant preferences for field $S$. rugosa over either forest $S$. rugosa or $S$. caesia but not for forest $S$. rugosa over $S$. caesia.) Dichomeris flavocostella and D. levisella trials were too few for analysis by Quade tests, but G tests (assuming eggs to be independent events) show highly significant preferences of $S$. rugosa in both cases ( $P<0.001$ ).

Table 3 have been previously reported from goldenrod-feeding Dichomeris species except the hyperparasite Dimmockia pallipes, which was reared from four parasitoids of $D$. levisella by Balduf (1969). Some closely related parasitoids have however been reared from goldenrodfeeding Dichomeris: Paralitomastix pyralidis (Ashmead) from D. flavocostella (Krombein et al., 1979), and Meteorus dimidiatus (Cresson), Oncophanes pusillus Muesebeck, Orgillus indigator Muesebeck, Pediobius sexdentatus (Girault), Temelucha sp. near epagoges, and Campoplex sp. from D. levisella (Balduf, 1969).

The reared Isomeris marginata in this study were all females. They emerged from fully grown caterpillars and spun a cylindrical brown cocoon, inside the tight leaf fold in which the host larva would have pupated. They closed both ends of the leaf fold (pupating Dichomeris larvae left the fold open at their anterior end). I reared some specimens from young larvae collected in late summer, which indicated that I. marginata oviposits in early instar caterpillars, and developing parasitoids overwinter inside the host larvae. Balduf (1969) gives further details on the biology and natural history of this parasitoid.

The common braconids (all three Apanteles spp., Meteorus sp., and Orgillus consuetus) also attacked in summer and overwintered in the host, but all emerged from Dichomeris caterpillars that were half to three-quarters grown. Apanteles spp. and $O$. consuetus greatly slowed the growth of the caterpillars, such that cocoons often did not appear in the leaf folds until July. Caterpillars parasitized by Meteorus sp. grew at a close to normal rate, and cocoons appeared in leaf folds in May or early June. As with the D. levisella caterpillars parasitized by Meteorus dimidiatus in Balduf's (1969) study, caterpillars from which a Meteorus sp. larva had emerged did not die for several days. They typically remained in the leaf fold with the parasitoid cocoon and did not feed, but they were capable of crawling if disturbed.

Among other frequent parasites, the eulophid Elarchertus argissa attacked caterpillars throughout the growing season. After killing the larva, the pinkish-green grub developed externally, feeding on the cadaver in the leaf fold. This polyphagous parasite was quite small (usually $<2 \mathrm{~mm}$ ), but its size was highly variable depending on the size of the host caterpillar.

The encyrtid, Paralitomastix sp., was the most frequent parasite of $D$. bilobella larvae. Host larvae developed normally, but in their final instar become extremely large and swollen, with several dozen wasp larvae (as many as 81). The parasitoids pupated within the dead caterpillar skin.

The rearings in this study for the recently described tachinid, Actia dimorpha (O'Hara, 1991) represent the only host records to date (J. E. O'Hara, pers. comm.). Maggots emerged from final instar caterpillars, one maggot per larva, and formed small brown puparia.

Among summer-hatching Dichomeris species, rates of parasitism varied widely ( $0-100 \%$, with the extremes encountered in smaller samples), but in large samples they were generally $40-50 \%$. Rates appeared similar between adjacent forests and fields, on $D$. ochripalpella (e.g., 22 of 51 specimens or $43 \%$ in forests, 17 of 33 specimens or $52 \%$ in fields, in two sampling areas in 1985). There were no obvious differences in rate of parasitism among the four common summer-hatching Dichomeris species, and most of the parasitoid species characterized as "frequent" (Table 2) were recovered from all four species.

The spring-appearing $D$. bilobella had a separate parasitoid complex. Its chief parasite was Paralitomastix sp., which did not attack the summer-hatching species. Conversely, most of the parasitoids of summer-hatching species did not attack D. bilobella (an exception was Actia dimorpha). Rates of parasitism of $D$. bilobella were low, often near $0 \%$; high rates occurred only in the dense population at Treman State Park, where $40 \%$ of $D$. bilobella larvae from a 1985 collection ( $\mathrm{N}=89$ ) succumbed to Paralitomastix sp .

## DISCUSSION

The present study brings to 14 the number of North American Dichomeris species known to feed on Solidago and its close relatives, with a total of 11 species reported from the northeastern United States. Additional Dichomeris species may well be present on these hosts; many species still lack host records and may have been missed to date because of rare or spotty distributions. Certainly the Dichomeris lineage is well-adapted to these hosts, given the large number of species known to use Solidago and Aster and their relative abundance among goldenrod-feeding Lepidoptera (Root, Loeffler, and Rawlins, unpubl.).

Powell (1980) pointed out that a given lepidopteran lineage may be characterized by a given level of feeding specialization. Evidence suggests that Dichomeris species are oligophagous, feeding on almost any species of Solidago, and perhaps on most species of Aster as well as other composites. In the laboratory, caterpillars generally accept whatever host plant species they encounter within this group, and their leaf-
Table 3. Parasitoids reared from Dichomeris larvae on Solidago, Euthamia, and Aster. Bilob $=$ D. bilobella, flavo $=D$. flavocostella, leuco $=$ D. leuconotella, levi $=D$. levisella, ochri $=D$. ochripalpella, nons $=D$. nonstrigella. Some caterpillars collected in early years of the study, or collected and reared in large groups to supply breeding stock, were not identified or were only identified as "flavocostella or leuconotella" if dark striped. Frequent $=$ reared from many specimens; somewhat frequent $=$ reared from $10-20$ specimens; infrequent $=$ reared from 3-10 specimens; rare $=$ reared from 1-2 specimens.

|  | Dichomeris species parasitized | Occurrence |
| :---: | :---: | :---: |
| Hymenoptera: Braconidae |  |  |
| Apanteles sp. 1, prob. undescribed | ochri, levi | frequent |
| Apanteles sp. 2 | not identified (mass collections) | somewhat frequent |
| Apanteles sp. 3 | flavo and/or leuco, and probably levi | somewhat frequent |
| Bracon gelechiae Ashmead | probably bilob (unidentifiable cadaver) | rare |
| Meteorus sp. possibly bakeri C.D. | flavo and/or leuco, levi, ochri, nons | frequent |
| Meteorus hyphantriae Riley | not identified (mass collection) | rare |
| Oncophanes sp. | flavo and/or leuco, unidentifiable cadavers | infrequent |
| Orgilus consuetus Muesebeck | flavo, leuco, ochri, probably levi | frequent |
| Possibly Rhysipolis sp. | ochri | rare |
| Hymenoptera: Eulophidae |  |  |
| Dimmockia pallipes Muesebeck | unidentified wasp cocoon from leuco | hyperparasite, rare |
| Elachertus argissa (Walker) | flavo and/or leuco, ochri, levi | frequent |
| Pediobius facialis (Giraud) | unidentified pupae | rare |
| Hymenoptera: Encyrtidae |  |  |
| Paralitomastix sp. | bilob | frequent |
| Ichneumonidae |  |  |
| Campoplex sp. | flavo and/or leuco, ochri | somewhat frequent |
| Coccygomimus aequalis (Prov.) or annulipes (Bralle) | leuco | rare |
| Diadegma sp. (one or two spp.) | bilob, flavo or leuco | rare |
| Exochus decoratus acitulus Prov. | bilob | rare |
| Isomeris marginata (Prov.) | flavo, leuco, ochri, and levi | frequent |

Table 3. Continued.

|  | Dichomeris species parasitized | Occurrence |
| :--- | :--- | :--- |
| Itoplectis conquisitor (Say) | cocoons of Isomeris marginata <br> and unidentified braconids <br> cocoon of Isomeris marginata <br> flavo and/or leuco, ochri, nons | hyperparasite, infrequent |
| Mesochorus vittator (Zett.) | flavo and/or leuco, nons, unidentified pupae | hyperparasite, rare |
| Temelucha platynotae (Cush.) | bilob, flavo, leuco | infrequent, specimens mostly from |
| Trichstus chosis Tow. | frequent |  |

folding behavior is flexible enough to allow them to use this moderately diverse array of hosts efficiently. Adults show more discrimination than larvae [a logical correlate of their greater mobility, also documented by Messina (1982) for the goldenrodfeeding chrysomelid beetle Trirabda virgata]. Consequently, distributions of larvae among host plant species in late summer, when adults choose the plants, differ from distributions in the following spring when the choice is made by larvae. In some cases (e.g., between $S$. altissima and $S$. rugosa), adult discrimination is based more on plant size than on plant species; but the avoidance of $S$. caesia by adults is striking; only $D$. bilobella regularly uses $S$. caesia as a host.

The Dichomeris species known to feed on goldenrods do not form a monophyletic lineage. Most such species are members of the large setosella species-group, but they are not closely allied within that group based on adult characteristics (Hodges, 1986). Dichomeris flavocostella is the most distantly related, being placed by Hodges (1986) in a different species-group; the resemblance of its caterpillars to those of other goldenrod-feeding species in color pattern, behavior, and phenology may be interesting examples of parallelism or convergence. Indeed, closer morphological study of the caterpillars of all members of both species-groups could be revealing, particularly after the host plant affinities of more species become known. Hodges (1986) identified two species pairs among the taxa discussed here, based on adult characteristics. These were 1) D. nonstrigella and D. purpureofusca, and 2) D. ochripalpella and $D$. achne. Larvae of $D$. purpureofusca and $D$. achne had not been reared before the present study. The larvae within each pair do show strong resemblances: $D$. nonstrigella and D. purpureofusca caterpillars share advanced phenology as well as wide bodies, small head capsules, and complex thoracic spot patterns; and D. ochripalpella and $D$. achne caterpillars share slender builds, similar coloration, and similar behavior (both form tight marginal leaf folds).

Observations from this study point out species differences which may have ecological as well as phylogenetic significance. For example, differences in the tightness of leaf folds are potentially linked to habitat use: in the northeast, tight folds are constructed only by the forest-inhabiting D. bilobella and D. ochripalpella and not by the species restricted to open habitats. However, reasons for this putative relationship remain unclear. Exposure of caterpillars of loose-folding and tight-folding species to forest and field predators, and monitoring of larvae transplanted to field and forest plants (Loeffler, 1992), gave no indication that loose folds provide superior protection in fields or that tight folds protect better in forests.

Subtle differences in phenology among summer-hatching species correlate with species abundance. Leaf-folding species hatching in July and overwintering as third or fourth instars (D. flavocostella, D leuconotella, D. levisella, and D. ochripalpella) were generally more widespread and common than those hatching in June and overwintering as fourth or fifth instars (D. agonia, D. nonstrigella, and D. purpureofusca). Any causal relationship must be based on timing rather than length of the life stages, because the stages are of similar lengths among June- and July-hatching species. Possible reasons might include improved adult reproduction, egg or larval survival, etc. later in the year.

Finally, a clear relationship was evident between parasitism and the unique phenology of $D$. bilobella. This spring species suffered relatively little parasitism and did not host most of the species that attacked summer-hatching Dichomeris caterpillars.

The interplay between developmental timing and parasitism could therefore play a major role in the phenological divergence of caterpillar lineages.

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# A REVISION OF THE SOUTH AMERICAN SPECIES OF THE ANT GENUS PROBOLOMYRMEX (HYMENOPTERA: FORMICIDAE) 

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#### Abstract

The South American species of the ant genus Probolomyrmex are revised. Three species boliviensis, brujitae, new species, and petiolatae are recognized. The synonymy of angusticeps with boliviensis is confirmed. A key to the species is given.


Probolomyrmex is a rare ant genus with pantropical distribution, comprising 13 species. So far, only two species were known from South America. The revision of the genus by Taylor in 1965 was based on few South American specimens from only two localities. With the exception of one nest series, all other specimens were taken as single ants in leaf litter samples or from rotten logs. However, it is more than likely that this genus belongs to a group of ants, which are more common than it appears from these collections. Ants living in leaf litter have only recently been given more attention, which led to the conclusion that the leaf litter might be the most diverse stratum for ants (e.g., Agosti et al., 1994; Belshaw and Bolton, 1994). However, there are not yet enough data to understand, whether there is a high faunal diversity between sites and thus a very high number of ant species as could be inferred from the South East Asian Myrmoteras (Agosti, 1992) with a very high degree of endemism, or a rather low as shown for West Africa by Belshaw and Bolton (1994). The latter observation is supported by recently collected Probolomyrmex specimens, including more localities indicating a much more extended distribution from Panama in the North to Argentina in the South.

Despite its scarcity, the species of this genus are well and comprehensively known through Taylor's revision in 1965 and Brown's additions (Brown, 1975). The sampling of recently collected series with workers and females confirmed the proposed synonymy of angusticeps with boliviensis (Brown, 1975), as well as the presence of a further species, brujitae, described below. P. brujitae is the most southern sample so far recorded in South America, and the first for Argentina, despite Kusnezov's thorough study of the Argentinian ant fauna (e.g., Kusnezov, 1978). However, the phylogeny of this genus is not yet understood.

This study aims at revising the South American species of Probolomyrmex based on all the available specimens from the following collections: American Museum of Natural History, New York, USA (AMNH); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); United States National Museum of Natural History, Washington, USA (USNM). The measurements are given in mm and follow those used by Taylor (1965:351): CI cephalic index (HW $\times 100 / \mathrm{HL}$ ), HL head length, HW head width, SL scape length, SI scape index (SL $\times 100 / \mathrm{HW}$ ), TL mesosoma length; all measurements are given in mm.


Figs. 1-14. 1-4. Probolomyrmex boliviensis. 1-2. Female (holotype): 1, head in full frontal view; 2, lateral view. 3-4. Worker (angusticeps syn.); 3, head; 4, lateral view. 5-6. brujitae, lateral view: 5, female (paratype); 6, worker (holotype). 7-8. petiolatus, lateral view: 7, female; 8, worker. 9-10. brujitae, head: 9, female (paratype); 10, worker (holotype). 11-12. petiolatus, head: 11, female; 12, worker. 13-14. Sculpture of lateral parts of first gastral tergite: 13, boliviensis; 14 , brujitae. All drawings of the same size except 13 and 14 , which are $2 \times$ larger.


Fig. 15. Probolomyrmex brujitae, holotype. The specimen was collected alive from a Winkler bag. The stretched out antennae with hardly any angle between the scape and the funiculus are typical.

## Genus Probolomyrmex Mayr

Probolomyrmex Mayr, 1901:2. Type species: Probolomyrmex filiformis Mayr, by monotypy. Taylor, 1965, revision.
Escherichia Forel, 1910:245. Type species: Escherichia brevirostris Forel, by monotypy. Syn. by Taylor, 1965:346.

A detailed and illustrated key to the genus is given by Bolton (1994), and a detailed diagnosis of the genus is provided by Taylor (1965). The long and slender body, the brown coloration, the finely or smoothly sculptured surface, the long sting, and foremost the socket-like base of the antennal insertion, unique among the ants, make this genus easily recognizable. Variation among the species is almost limited to changes in shape of the head and scape, the petiole and to a lesser degree, the body sculpture. In the field, the species are recognized by their very fast, straight movements, the stretched out antennae (Fig. 15), and that they are mainly found as singletons.

## KEY TO THE SPECIES <br> (Worker and females)

1 Petiole in lateral view with a ventral, rectangular process (Figs. 7, 8) .......... petiolatus

- Petiole in lateral view with a ventral process directed towards the mesosoma (Figs. 2, 4-6)
2 Small body size (TL $<0.95 \mathrm{~mm}$ ), short scape (SI < 105). Sculpture fine and densely set (Fig. 14). First gastral segment ventrally without a collar. Head with a bulge along the posterior ventral face, which, in lateral view is not darker than the adjacent surface. Ventral process of petiole in lateral view of the same color as the adjacent tergite .. brujitae
- Larger body size (TL > 0.95 mm ), longer scape (SI > 105). Sculpture with large pits with chagrination in between (Fig. 13). First gastral segment ventro-anterior with a distinct collar which is bent ventrally (Figs. 2, 4). Head with a distinct carina along the posterior ventral face, which is darker than the adjacent surface. Ventral process of petiole in lateral view distinctly more darkly colored than the tergite boliviensis


## Probolomyrmex boliviensis Mann

boliviensis Mann 1923:16. Holotype female, BOLIVIA, Beni, Rurrenabaque, W. M. Mann. USNM type 25906. Description of larva, pupa and biology: Taylor, 1965: 348-9, 360-1 [checked].
angusticeps M. R. Smith 1949:39. Syntypes 2 workers, Panama, Barro Colorado Island, Zetek \#5272. Smithsonian type 58833 [checked]. Synonymy by Brown, 1975:11 [see also note 22 in Brown, 1975:57]. Synonymy confirmed.

FEMALE. HL 0.67-0.70, HW 0.45-0.5, SL 0.47-0.61, TL 0.98-1.06, CI 65-69, SI 105-123, Figures 1-2 (3 examined).

WORKER. HL $0.68-0.82$, HW $0.42-0.47$, SL $0.50-0.64$, TL $0.96-1.25$, CI 5762, SI 119-136, Figures 3-4 (15 examined).
Material examined. 18 workers, 3 females, deposited in MCZ and USNM. PANAMA, Barro Colorado Island, Canal Zone, 21 June 1961, R. W. \& W. Taylor; PANAMA,
pipeline road, Gamboa, 1976, Sclavings. COLOMBIA, Magdalena, Tayrona PK, Pueblito, 1 October 1976, Berlese sample, leaf litter, C. Kugler. PERU, Madre de Dios, Cuzco Amazonico, 15 km NE of Puerto Maldonaldo, 200 m , Terra Firme forest, plot 1U15, rotten chunk of wood half buried in soil, 22 June 1989, S. P. Cover \& J. Tobin.
Comments. This is the largest of the South American species. It is easily diagnosed by the combination of its mesosoma size, the short scape and the very distinct sculpture. The synonymy could be confirmed through a series of workers and females. The biology of boliviensis is described in detail by Taylor (1965), but many questions such as nutritional base need to be answered. This species occurs in rainforests of northern South America, from Panama to Bolivia.

## Probolomyrmex brujitae, new species

Holotype 1 worker, Argentina, Jujuy, Aguas Blancas-Yaculica (Argentinian-Bolivian Frontier), $22^{\circ} 43^{\prime} 44^{\prime \prime} \mathrm{S} 64^{\circ} 22^{\prime} 25^{\prime \prime}$ W, $460 \mathrm{~m}, 25$ October 1994, D. Agosti \& J. M. Carpenter, Winkler sample, leaf litter, Yungas forest. Holotype deposited in MCZ.

Paratype 1 female, same Winkler sample as holotype. Deposited at Instituto Miguel Lillo Tucumán.

FEMALE. HL 0.57, HW 0.35, SL 0.35, TL 0.85, CI 62, SI 100, Figures 5, 9 (1 examined).

WORKER. HL 0.60, HW 0.36, SL 0.35, TL 0.81 , CI 60, SI 99, Figures 6, 10, 14, 15 (1 examined).
Material examined. Holotype and paratype.
Comments. This species is easily recognized by its small size, the fine sculpture, and the shape and color of the ventral petiolar process which is the same as the one of the petiolar tergite. The specimens were collected by Winkler bags using sifted leaf litter from a secondary Yungas forest, and this species is only known by the two type specimens collected in the same locality.

## Probolomyrmex petiolatus Weber

petiolatus Weber, 1940:76. Holotype worker, Panama, Barro Colorado Island [specimen from BCI compared with the type checked by S. Cover].

FEMALE. HL 0.61, HW 0.42, SL 0.44, TL 0.90. CI 70, SI 104, Figures 7, 11 (1 examined).

WORKER. HL 0.51-0.64, HW 0.35-0.40, SL 0.31-0.41, TL 0.66-0.88, CI 6369, SI 70, Figures 8,12 ( 2 examined).
Comments. This species is easily recognized by the subpetiolar process. The new samples expand the known distribution range well into northern South America. Nothing is known of the biology of this species.
Material examined. 2 workers and 1 female, deposited in MCZ and USNM. PANAMA, Barro Colorado Island; leaf litter, forest floor; A. Newton. COLOMBIA, Meta, Quebrada Susamuko, 23 km NW Villavicencio, 1,000 m, leaf litter, March 5, 1972, J. Peck. VENEZUELA, T. F. Amazonia, Cerro de la Neblina, basecamp, 140 m , $0^{\circ} 50^{\prime} \mathrm{N} 66^{\circ} 10^{\prime} \mathrm{W}, 10-20$ February 1985, flight intercept pan trap in rainforest, P. J. Spangler et al.

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# LARVAL DESCRIPTION OF ABARIS BIGENERA BATES, 1882, AND NOTES ON RELATIONSHIPS OF THE GENUS ABARIS DEJEAN, 1831 (COLEOPTERA: CARABIDAE: PTEROSTICHINI) 

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#### Abstract

The three larval instars of the Neotropical Abaris bigenera Bates, 1882, are described. Based on this first larval description for the genus, Abaris larvae share two synapo-morphies-extremely short coronal suture, and ventrally extended membranous band on the maxillary stipes-with the Mediterranean pterostichine genus Orthomus Chaudoir, 1838, suggesting that they are closely related.


The genus Abaris Dejean, 1831, is a small New World genus belonging to the large and complex tribe Pterostichini. It includes nine species that range from Arizona and southeastern California south to Brazil. Only one species, Abaris splendidula (LeConte, 1863), has been found north of Mexico.

Little is known about the taxonomy and bionomics of Abaris species. Straneo (1939) wrote a key to the species excluding A. splendidula, and Bousquet (1984) redescribed $A$. splendidula and compared it with the other Mexican species. Larvae of Abaris were previously unknown.

This paper describes the larvae of $A$. bigenera Bates, 1882, and briefly discusses the relationship of the genus. Abaris is the first Neotropical Pterostichini genus-group taxon to be described in its larval stage.

## MATERIALS AND METHODS

The description of Abaris bigenera Bates is based on 16 larvae $\left(5 \mathrm{~L}_{1}, 5 \mathrm{~L}_{2}, 6 \mathrm{~L}_{3}\right)$ reared ex ovo from adults collected at 18.3 km S Guelatao, Oaxaca, Mexico. Larvae are deposited in the Canadian National Collection of Insects and Arachnids, Ottawa, and Cornell University Insect Collection, Ithaca (Lot No. JKL-88H16.5).

Larvae were cleared in hot $10 \% \mathrm{KOH}$, impregnated with glycerine (see Goulet, 1977), and studied with an interference contrast microscope at 100-400×.

Terms used for structures have been explained previously (Bousquet, 1985); notation of primary setae and pores follows Bousquet and Goulet (1984), and notation of secondary setae follows Bousquet (1985).

Larvae of the following pterostichine genus-group taxa were available for comparison: Orthomus Chaudoir, Poecilus Bonelli, Derus Motschulsky, Lophoglossus LeConte, Gastrellarius Casey, Stereocerus Kirby, Myas Dejean, Lagarus Chaudoir, Argutor Dejean, Bothriopterus Chaudoir, Melanius Bonelli, Pseudomaseus Chaudoir, Monoferonia Casey, Platysma Bonelli, Morphnosoma Lutshnik, Abacidus LeConte,


Fig. 1. Dorsal habitus of Abaris bigenera, $\mathrm{L}_{3}$.

Steropus Dejean, Feronidius Jeannel, Cylindrocharis Casey, Oreophilus Chaudoir, Hypherpes Chaudoir, Cryobius Chaudoir, Cyclotrachelus Chaudoir, Abax Bonelli, and Molops Bonelli.

## LARVAL DESCRIPTION OF ABARIS BIGENERA BATES

Diagnosis. Larvae of Abaris bigenera differ from those of other known New World Pterostichini by the absence or extreme reduction of the coronal suture (Figs. 1, 2). This character state occurs in several groups of Platynini whose larvae are structurally similar to those of Pterostichini. Larvae of $A$. bigenera, however, differ from those of Platynini by the apically acuminated lacinia in combination with the membraneous area extended over the ventral side of the stipes in second and third instars (Fig. 3). Description. First instar. With the characteristic features of the tribe Pterostichini as outlined by Bousquet (1985), plus the following. Head width: 0.47-0.49 mm. Microsculpture: Frontale, parietale, and pronotum without microsculpture. Mesonotum and metanotum with multipointed microsculpture over anterior third of posterodiscal area. Tergites I-IX with multipointed, in part pointed laterally, microsculpture all over posterodiscal area (though very sparse on posterior half of first tergite). Urogomphi with pointed microsculpture all over. Chaetotaxy: Adnasale, prementum, and femur without additional setae. Seta $\mathrm{FR}_{2}$ on frontale long; seta $\mathrm{FR}_{4}$ anterior to level of $\mathrm{FR}_{\mathrm{c}}$. Seta $\mathrm{PA}_{4}$ on parietale $0.2-0.3 \times$ length of $\mathrm{PA}_{7} ; \mathrm{PA}_{5}$ very small, subequal in length to $\mathrm{PA}_{1}-\mathrm{PA}_{3}$; seta $\mathrm{PA}_{6} 0.3-0.4 \times$ length of $\mathrm{PA}_{7}$; pore $\mathrm{PA}_{\mathrm{b}}$ on parietale lateral to level of $\mathrm{PA}_{4}$. Length of seta $\mathrm{MX}_{6}$ on lacinia subequal to that of $\mathrm{MX}_{5}$; setal group gMX with about 30 setae. Setae $\mathrm{PR}_{3}$ and $\mathrm{PR}_{11}$ on pronotum distinct; seta $\mathrm{PR}_{12}$ distinct, its length about $0.7 \times$ that of $\mathrm{PR}_{11}$. Setae $\mathrm{ME}_{12}$ on mesonotum and metanotum distinct; seta $\mathrm{ME}_{13}$ distinct, its length $0.6-0.7 \times$ that of $\mathrm{ME}_{12}$. Setae $\mathrm{TE}_{1}, \mathrm{TE}_{6}$ and $\mathrm{TE}_{7}$ on tergites I-VII subequal in length; seta $\mathrm{TE}_{10}$ on abdominal tergite I-VIII distinct, its length $0.7-0.9 \times$ that of $\mathrm{TE}_{9}$. Seta $\mathrm{UR}_{2}$ on abdominal tergite IX at least $7 \times$ longer than $\mathrm{UR}_{3}$. Urogomphus with 5 long setae $\left(\mathrm{UR}_{4}-\mathrm{UR}_{8}\right)$. Head: Nasale more or less straight. Egg-bursters not extended to level of seta $\mathrm{FR}_{2}$, consisting of about 5 microspinulae. Frontal suture between levels of $\mathrm{FR}_{2}$ and egg-bursters oblique; coronal suture absent. Parietale with 6 ocelli on each side. Cervical sulcus present, extended dorsally to level of seta $\mathrm{PA}_{7}$. Antennomere I without membranous area near base. Mandible moderately curved; retinaculum narrow; medial margin of terebra smooth. Stipes $1.8-1.9 \times$ as long as wide; membranous area restricted to lateral side of stipes; length of maxillary palpomere II $1.6-1.7 \times$ that of palpomere III. Ligula well developed. Legs: Claws subequal in length. Abdomen: Urogomphi slightly curved medially in apical half. Abdominal pleura without additional sclerite in front of epipleurite.
Second instar. Similar to third instar except for the following states. Head width: $0.64-0.65 \mathrm{~mm}$. Head: Antennomere I about $2 \times$ longer than antennomere II, about $1.1 \times$ longer than antennomere III, and about $1.3 \times$ longer than antennomere IV. Stipes $2.1-2.2 \times$ as long as wide.
Third instar. With the characteristic of the tribe Pterostichini, as outlined by Bousquet (1985), plus the following. Head width: $0.97-0.98 \mathrm{~mm}$. Microsculpture: Frontale, parietale, pronotum, mesonotum, metanotum, and abdominal tergites I-IV without distinct microsculpture pattern; tergites V-VII with faint, sparse, progressively more


Figs. 2-4. Abaris bigenera, $\mathrm{L}_{3}$. 2. Cephalic capsule, prementum and labial palps, left mandible, and left antenna (dorsal view). 3. Left maxilla (ventral view). 4. Abdominal tergite IX and urogomphi (dorsal view).
developed pointed microsculpture anterolaterally on posterodiscal area; tergite VIII with faint, pointed to multipointed microsculpture over entire posterodiscal area. Urogomphi with pointed microsculpture all over, sparser apically. Chaetotaxy: Adnasale with 2 setae $\left(\mathrm{FR}_{8}-\mathrm{FR}_{9}\right)$. Seta $\mathrm{FR}_{2}$ on frontale long; seta $\mathrm{FR}_{4}$ anterior to level of $\mathrm{FR}_{\mathrm{c}}$. Seta $\mathrm{PA}_{4}$ on parietale $0.1-0.2 \times$ length of $\mathrm{PA}_{7} ; \mathrm{PA}_{5}$ very small, subequal in length to $\mathrm{PA}_{1}-\mathrm{PA}_{3}$; seta $\mathrm{PA}_{6} 0.4-0.6 \times$ length of $\mathrm{PA}_{7}$; pore $\mathrm{PA}_{\mathrm{b}}$ on parietale lateral to level of $\mathrm{PA}_{4}$. Antennomere I and II without setae. Mandible with 2 lateral setae ( $\mathrm{MN}_{1}$ and $\mathrm{MN}_{\alpha}$ ). Length of seta $\mathrm{MX}_{6}$ on lacinia $0.8-1.0 \times$ that of $\mathrm{MX}_{5}$; setal group gMX with less than 50 setae. Setae $\mathrm{PR}_{3}$ and $\mathrm{PR}_{11}$ on pronotum distinct; seta $\mathrm{PR}_{12}$ also distinct, its length $0.8-1.0 \times$ that of $\mathrm{PR}_{11}$. Seta $\mathrm{ME}_{12}$ on mesonotum and metanotum distinct; seta $\mathrm{ME}_{13}$ also distinct, its length $0.8-1.0 \times$ that of $\mathrm{ME}_{12}$. Tibia without secondary setae. Abdominal tergites I-V without numerous secondary setae; seta $\mathrm{TE}_{\alpha}$ distinct on abdominal tergites I-VII. Seta $\mathrm{UR}_{2}$ on abdominal tergite IX (Fig. 4) at least $7 \times$ longer than $U R_{3}$. Urogomphus (Figs. 1, 4) with 9 long setae $\left(\mathrm{UR}_{4}-\right.$ $\mathrm{UR}_{8}, \mathrm{UR}_{\beta} \mathrm{UR}_{\gamma}, \mathrm{UR}_{\delta}, \mathrm{UR}_{\epsilon}$ ). Head: Nasale more or less straight (Figs. 1, 2). Coronal suture extremely short, more or less distinct. Parietale with 6 ocelli on each side. Ocular sulcus absent. Cervical groove present, not extended laterally beyond level of $\mathrm{PA}_{15}$. Antennomere I without membranous area near base; antennomere I about $1.7 \times$ longer than antennomere II, about $1.2 \times$ longer than antennomere III, and about $1.7 \times$ longer than antennomere IV. Mandible moderately curved; penicillus present; retinaculum narrow; medial margin of terebra smooth. Stipes (Fig. 3) 2.4$2.5 \times$ as long as wide; membranous area extended over entire width of ventral side of stipes (though less distinct medially); length of maxillary palpomere II 1.9-2.0× that of palpomere III. Ligula well developed. Legs: Claws subequal in length. Abdomen: Urogomphi less than $4 \times$ as long as tergite IX, slightly curved medially in apical half. Abdominal pleura without additional sclerite in front of epipleurite.
Life cycle data. Three adults ( 299,16 ) were collected in the field on 16 August 1988, and maintained in a cooler until returned to the laboratory about one week later. In the laboratory, adults were maintained at $13: 11 \mathrm{~L}: \mathrm{D}$ at $22^{\circ} \mathrm{C}$ day, $20^{\circ} \mathrm{C}$ night, and fed mealworm chunks 2-3 days/week. The first $L_{1}$ larvae were seen 5 September and the last of the 16 was first observed on 6 October.

The average duration of the first instar under the same environmental and feeding regime was 5.6 days $(\mathrm{N}=12)$. The duration of the second instar averaged 7 days ( N $=6$ ). No third instar larvae were reared to the pupal stage.

## DISCUSSION

Relationships of Abaris have never been addressed. Bates (1882:85) noted that the Mexican and South American Pseudabarys Chaudoir, 1873 are "very closely allied to Abaris." He also stated about Pseudabarys that "its nearest ally in the New World is probably Ophryogaster." Bates further reported the comments of Chaudoir (1873: 99) considering Pseudabarys closely related to the Mediterranean genus Orthomus Chaudoir and the Australian genera Simodontus Chaudoir and Ceneus Chaudoir (regarded today as a junior synonym of Prosopogmus Chaudoir).

In most recent classifications, such as Csiki (1930), Reichardt (1977), and Straneo (1977), Abaris is placed near Abaridius Chaudoir and Pseudabarys. Abaridius com-
prises a single species from Brazil that was originally described as a member of Abaris, and Pseudabarys includes seven species from Mexico and South America.

Compared with larval stages of the taxa studied, Abaris larvae are phenetically very similar to those of Orthomus. More importantly, Orthomus larvae have no ( $\mathrm{L}_{1}$ and $L_{2}$ ) or an exceedingly short ( $L_{3}$ ) coronal suture, a character state elsewhere found among pterostichines only in Abaris. Also within Orthomus larvae, the ventral membranous area of the stipes extends over the entire width in $L_{2}$ and $L_{3}$, a configuration shared with Abaris larvae. In other pterostichine larvae, the membranous area of the stipes is either lateral, or extends ventrally only on the lateral half of the stipes, very rarely over the entire width. Occurrence of these two character states, i.e., short to absent coronal suture and extended membraneous area of stipes, both likely synapomorphic, suggests that Abaris is closely related to the genus Orthomus. All other character states of Abaris and Orthomus larvae, except for a few such as the microsculpture and egg-burster shape in which the transformation polarity is difficult to assess, are probably plesiomorphic for the Pterostichini.

The genus Orthomus is restricted to the Mediterranean region and includes about 30 species assigned to five subgenera, Orthomus sensu stricto, Nesorthomus Bedel, Eutrichopus Tschitschérine, Wolltinerfia Machado, and Trichopedius Bedel. Several of these taxa are ranked as genera by some authors.

Arndt and Hurka (1990) suggested that Orthomus could be closely related to the Holarctic taxon Lagarus (considered a subgenus of Pterostichus Bonelli by most authors) based on larval states of straight nasale and long seta $\mathrm{MX}_{6}$. Both features also occur in larvae of Abaris as well as in many other pterostichine taxa and, in our opinion, are plesiomorphic for pterostichines. Furthermore, adult structures indicate that Orthomus and Lagarus are not closely related. Lagarus belongs to a large clade composed of several genus-group taxa including Pterostichus; the clade is autapomorphic for the presence of a transverse apophyse on the left paramere (Bousquet, unpbl.). Members of Orthomus and Abaris have no such apophyse on the left paramere.

Larvae of the Neotropical genera Abaridius and Pseudabarys, and of the Australian Simodontus and Prosopogmus are unknown.

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# A REVIEW OF THE GENUS PSEUDEVOPLITUS RUCKES, (HETEROPTERA: PENTATOMIDAE) WITH THE DESCRIPTION OF THREE NEW SPECIES 

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#### Abstract

Pseudevoplitus Ruckes is revised on the basis of morphological characters with emphasis on the genitalia of both sexes. Four species are recognized, three of them new: $P$. paradoxus Ruckes, 1958, P. costalimai, n. sp., P. peruvianus, n. sp., and $P$. vittatus, n. sp. The species P. longicornis Ruckes, 1959, P. casei Thomas, 1980, and P. mexicanus Brailovsky and Barrera, 1982 are transferred to a new genus, described in another paper. Key Words. - Pentatomidae, Pseudevoplitus, neotropical, taxonomy, stinkbug.


The genus Pseudevoplitus was described by Ruckes (1958) for P. paradoxus based on male and female specimens from Peru. Ruckes (1959) later described a second species, $P$. longicornis from Panama. More than two decades later two species were added, one by Thomas (1980), P. casei from Guatemala, and another by Brailovsky and Barrera (1982), P. mexicanus, from Mexico. The last two species are closely allied to $P$. longicornis. A detailed examination of the genitalia of both sexes, as well as the discovery of three new species, allied to $P$. paradoxus, has persuaded us to exclude P. longicornis, P. casei, and P. mexicanus from Pseudevoplitus and erect a new genus described in a separate paper. Grazia et al. (1993) have previously discussed the relationship between Evoplitus Amyot and Serville and Pseudevoplitus.

Members of the genus Pseudevoplitus possess an anteriorly-directed spine on the 3rd abdominal sternite in apposition to a posteriorly-directed, bifid process on the metasternite, thus placing the genus in section three of the Pentatomini (sensu Rolston et al., 1980).

Pseudevoplitus has a mainly northern distribution in South America, being represented in Peru, Bolivia and northern Brazil. P. paradoxus has the widest known distribution of any species, ranging from Peru to central Argentina.

## MATERIAL AND METHODS

Measurements are given in millimeters and correspond to the mean for all specimens studied. Length was measured along the midline from the tip of the tylus to the apex of the seventh abdominal segment. Length and width of each gonocoxite 8 of the female genital plates were taken on the extreme, maximal points touched by imaginary lines. The terminology for the structure of the genitalia was adopted from Dupuis (1970) and Schaefer (1977). The genitalia were treated with $10 \% \mathrm{KOH}$, and stained in Congo Red.

Specimens are deposited with the following institutions with their acronyms as they appear in the text: AMNH-American Museum of Natural History, New York, NY; DAR - David A. Rider Collection, Fargo, ND; DBT—Donald B. Thomas Collection, Weslaco, TX; LACM - Los Angeles County Museum of Natural History, Los Angeles, CA; MCNZ—Museu de Ciências Naturais, FZBRS, Porto Alegre RS, Brasil.

Pseudevoplitus Ruckes, 1958
Pseudevoplitus Ruckes, 1958:8-9; Thomas, 1980:293; Brailovsky and Barrera, 1982: 231-232; Brailovsky, 1988:131.

Type species: Pseudevoplitus paradoxus Ruckes, 1958, by original designation.
Ruckes' (1958) description is augmented as follows: Length of head almost half the width across eyes. Juga and tylus equal in extent or juga slightly longer than tylus.

Antennal segment I almost attaining or clearly exceeding apex of head. Bucculae moderately prominent, rectilinear in profile, margins elevated anteriorly, parallel, then gradually becoming lower, in ventral view divergent posteriorly. Humeri produced; antero-lateral margins thick, obtuse, irregularly crenulate or subtuberculate. Rostrum with segment I lying in sulcus between bucculae; II arcuate, surpassing procoxae; last two segments dorso-ventrally depressed. Venation of membrane brown; intervenal membrane mostly transparent. Connexivum widely exposed, apical angles acutely produced; segments III to VI with attendant minute spine immediately mesad to each apical angle; angle of segment VII subacuminate, also bearing acute, dorsal, rearwardly projecting spinous process. Posterior margin of metasternal plate excavated in triangular notch to receive anteriorly directed protuberance of third abdominal segment. Spiracles oval.
Male genitalia: Pygophore widely open, anterior chamber of genital capsule (sensu Schaeffer, 1977) ample; posterolateral angles expanded; dorsal border deeply excavated, fully exposing segment X (proctiger); ventral rim deeply $U$-shaped excavated, ventral wall depressed behind excavation; infolding of ventral rim dilated on each side of excavation. Diaphragm very finely striated, striae parallel; $1+1$ keel-like, strongly sclerotized processes projecting from dorsal border of pygophore to base of parameres; processes in dorsal view, noticeable halfway between midline of dorsal border and posterolateral angles of pygophore. Longitudinal axis of proctiger perpendicular to sagittal plane of pygophore; anal tube opening ventrally; basal part of proctiger expanded into ample, nearly bilobate process; distal portion of process visible in ventral view, obscuring body of proctiger in dorsal view. Parameres simple, elongate, semi-erect, acutely tipped and curving toward proctiger. Phallotheca cylindrical, open posteriorly, bearing two processes: basal one (processus phallothecae 1), subrectangular, posterior margin notched at midline, and second one (processus phallothecae 2), at distal aperture, projecting dorsally, voluminous, resembling stretched tongue. Basal plates of articulatory apparatus with two pairs of connectives on dorsal side; internal pair flat, large relative to basal plates when combined with processus capitati. Ponticulus transversalis projecting as long, semi-membranous sheath, laterally continuous with dorsal connectives. Ductus seminis distalis short, enveloped by voluminous vesica which bears dorsally a pair of recurved arms (processus vesicae). Female genitalia: Sternite VII produced into strong, spine-like projection; imaginary
transverse line touching apices of laterotergites 9 crosses sternite VII far from its apex. Distance between this imaginary line to apex of sternite VII about twice medial length of segment X. Posterior border of sternite VII semicircularly excavated on gonocoxites 8, oblique, truncate on laterotergites 9 . Abdomen in profile, forming an obtuse angle between intersection of two imaginary planes tangential respectively to midlongitudinal abdominal keel, and gonocoxites 8 . Gonocoxites 8 feebly tumescent or almost flat, surface bearing faint, linear rugulae emitting obliquely from sutural borders which are parallel for $2 / 3$ to $3 / 4$ of length basally, divergent distally; posterior border truncated. Laterotergites 9 narrowly triangular, well surpassing transverse band uniting laterotergites 8 dorsally. Posterior border of laterotergites 8 produced into acute lobe. Anterior margin of gonocoxites 9 nearly uniformly concave; anterolateral angles somewhat expanded anteriorly. Thickening of vaginal intima not uniformly sclerotized, sclerotization restricted to wide basal ring. Chitinellipsen large, lying on each side of thickening of vaginal intima. Portion of ductus receptaculi preceding vesicular area about twice as long as portion after. Capsula seminalis subconical bearing three digitoid projections. Pars intermedialis constricted at distal third; anterior and posterior annular crests, each with well developed flange.

## KEY TO THE SPECIES OF PSEUDEVOPLITUS

1. Humeri strongly produced into cornute spines. Posterior borders of gonocoxites 8 obliquely truncate, sutural borders truncately divergent distally (Figs. 19, 21)

- Humeri acutely produced. Posterior borders of gonocoxites 8 transversely truncate, sutural borders arcuately divergent distally (Fig. 20)

2. Dorsal surface matte, tan, with dark brown, longitudinal vitta on midline of pronotum and scutellum (Fig. 1). Pygophore with minute spine immediately dorsad of each posterolateral angle (Figs. 13, 15). Outline of diaphragm process in form of a quadrangular projection at dorsal border of pygophore, projecting nearly to base of paramere (Fig. 13). Posterior border of gonocoxites 9 bilobate (Fig. 21) ..... P. vittatus n. sp.

- Dorsal surface tan with dark brown markings nebulous, irregularly distributed on pronotum, scutellum and hemelytra. Pygophore without minute spine near posterolateral angles. Diaphragm process in form of a spatulate projection at dorsal border of pygophore, not projecting to base of paramere (Figs. 6, 11). Posterior border of gonocoxites 9 arcuately concave (Fig. 19)
P. paradoxus Ruckes

3. Juga slightly but distinctly longer than tylus (Fig. 2). Basal antennal segment not quite attaining apex of head. Eyes smaller, diameter approximately half width of head at anterior one-third. Diaphragm process oblique at dorsal border of pygophore, projecting about one-third distance from dorsal border to base of paramere (Figs. 4, 10)
P. costalimai n . sp .

- Juga and tylus equal in apical extent (Fig. 3). Basal antennal segment clearly exceeding apex of head. Eyes large, diameter approximately equal to width of head at anterior one-third. Outline of diaphragm process in a triangular projection at dorsal border of pygophore (Fig. 8), halfway from dorsal border to base of paramere (Fig. 12)
P. peruvianus n . sp .


## Pseudevoplitus paradoxus Ruckes, 1958

(Figs. 6, 7, 11, 16-19, 22)
Pseudevoplitus paradoxus Ruckes', 1958:9-12; Ruckes, 1959:17; Thomas, 1980:296;
Brailovsky and Barrera, 1982:231-234.


Fig. 1. Psendevoplitus vittatus, n. sp., dorsal habitus.

We make the following correction to Ruckes' (1958) description for the length of the antennal segments: segment IV longest, segments II, III, and V subequal, each more than twice the length of segment I (basal).
Male: Postero-lateral angles of pygophore obliquely truncate in ventral view (Fig. 7); lateral borders of median excavation of ventral rim incrassate. Diaphragm process


Figs. 2, 3. Head and pronotum. 2. Pseudevoplitus costalimai, n. sp. 3. P. peruvianus, n. sp.


Figs. 4-9. Male pygophore. 4, 5. P. costalimai, n. sp. 4. Dorsal view. 5. Ventral view. 6, 7. P. paradoxus Ruckes. 6. Dorsal view. 7. Ventral view. 8, 9. P. peruvianus, n. sp. 8. Dorsal view. 9. Ventral view. ( $\mathrm{DB}=$ dorsal border, $\mathrm{DVW}=$ depression of ventral wall, $\mathrm{ER}=$ excavation of ventral rim, $\mathrm{IR}=$ infolding of ventral rim, $\mathrm{Par}=$ paramere, $\mathrm{PLA}=$ postero-lateral angles, PrD $=$ process of diaphragm, Pro $=$ proctiger, PrPro $=$ process of proctiger, $\mathbf{S}=$ spine of dorsal border.)


Figs. 10-15. Male pygophore. 10. P. costalimai, n. sp., posterior view. 11. P. paradoxus Ruckes, posterior view. 12. P. peruvianus, n. sp., posterior view. 13-15. P. vittatus, n. sp. 13. Dorsal view. 14. Ventral view. 15. Posterior view.
in form of a spatulate projection at dorsal border of pygophore, not projecting to base of paramere (Figs. 6, 11). Paramere scythe-shaped. Basal process of proctiger in dorsal view apparently bilobate, each lobe slightly convex, posterior margin convexly arcuate. Phallus as illustrated (Figs. 16-18).
Female: Gonocoxites 8 approximately one-fourth longer than wide, disc flat, rugulose; sutural borders parallel along basal two-thirds, distal third truncately divergent; posterior border obliquely truncate, external angle more posteriorly projected than sutural angle; external borders nearly rectilinear (Fig. 19). Spiracles of laterotergites 8 present, visible. Gonocoxites 9 flat, posterior border nearly concave. Ectodermal genital ducts as illustrated (Fig. 22).


Figs. 16-20. Male genitalia of Pseudevoplitus paradoxus Ruckes. 16. Phallotheca, lateral view. 17. Phallus, dorsal view. 18. Phallus, ventral view. 19, 20. Female genital plates, ventral view. 19. P. paradoxus Ruckes. 20. P. peruvianus, n. sp. ( $\mathrm{BP}=$ basal plates, $\mathrm{DC}=$ dorsal connectives, Gc8 $=$ gonocoxites 8 , Gc9 $=$ gonocoxites $9, \mathrm{GS}=$ secondary gonopore, $\mathrm{La} 8=$ laterotergites $8, \mathrm{La} 9=$ laterotergites $9, \mathrm{Me}=$ Membranblase, $\mathrm{PCa}=$ processus capitati, $\mathrm{Ph}=$ phallotheca, $\mathrm{PrPhl}=$ processus phallothecae $1, \operatorname{PrPh} 2=$ processus phallothecae $2, \mathrm{Pr} \mathrm{V}=$ processus vesicae, $\mathrm{PT}=$ ponticulus transversalis, $\mathrm{V}=$ vesica, VII $=$ sternite VII, $\mathrm{X}=$ segment X .)


Figs. 21, 22. Female genitalia. 21. Genital plates of $P$. vittatus, n. sp. 22. Female ectodermal genital ducts of $P$. paradoxus. $(\mathrm{AAC}=$ anterior annular crest, $\mathrm{Ch}=$ Chitinnelipsen, $\mathrm{CS}=$ capsula

Distribution: Peru, Brazil, Bolivia, and Argentina.
Holotype: Male deposited in AMNH was examined, labeled: (a) Tingo Maria, Huan., Peru, November 23, 1946, Alt. 2,200 ft (b) J. C. Pallister Coll. Donor Frank Johnson (c) AMNH (d) Pseudevoplitus paradoxus Ruckes Holotype.

Allotype: Female deposited in AMNH also examined, labeled: (a) Peru, Monson Valley, Tingo Maria, X-12-1954 (b) E. I. Schlinger and E. S. Ross collectors (c) Pseudevoplitus paradoxus Ruckes Allotype.
Paratypes: One male, same data as allotype except date X-9-1954; one female same data as holotype except date January 11, 1947 both deposited in AMNH.
Additional material: One male, BRAZIL, Rondonia, 62 km SW Ariquemes nr Fazenda Rancho Grande, XII-6/15-1990, D. A. Rider and J. E. Eger, collected at light (DBT); one male, BOLIVIA, Chuguisaca, 30 km SE Carandaity, VIII-1957, Stephen C. Bromley (LACM); one male, ARGENTINA, Misiones, Puerto Iguazu, XII-1991 (DAR).

Pseudevoplitus costalimai, new species
(Figs. 2, 4, 5, 10)
Description: Elongate oval, dorso-ventrally depressed with pronotum somewhat gibbous and humeral angles prominent. Dorsal color mottled tan.
Male: Measurements. Length of head 2.72; anteocular length 1.60; width of head 2.88; width between eyes 1.56 ; width between ocelli 0.76 ; antennal segment I 1.04 , II 1.40 , III 2.20 , IV 2.80 , V missing; pronotal length 3.77 ; width across humeri 6.72 (without spines), 8.11 (with spines); scutellar length 5.24 ; basal width 4.59 ; total length 13.94 ; width across third abdominal segment 7.62.
Head: Yellow-tan dorsally with irregularly disposed reddish-brown punctures. Juga slightly longer than tylus with internal margins subparallel, external margins slightly convergent, mildly reflexed, dark brown, apices obtuse (Fig. 2). Width across eyes about equal to length along midlongitudinal line. Anterior border of bucculae in lateral view slightly convex. Rostrum very long, attaining base of abdominal sternite VII in repose, segment III almost 1.5 times length of IV. Antennal segment I almost attaining apex of head, segment IV longest, slightly longer than V. Ocelli large, each separated from adjacent eye by diameter of ocellus.
Thorax: Pronotum yellow-tan with many reddish-brown, irregularly disposed punctures over posterior half, large, transverse band of concentrated ferrugineous punctures behind cicatrices. Humeri produced as triangular spine, curving posteriorly; anterior two-thirds of anterolateral pronotal margins irregularly crenulate (Fig. 2). Scutellum yellow-tan with reddish-brown punctures irregularly distributed, darker and more concentrated basally and laterally; apex acute. Hemelytra yellow-tan with reddish-brown punctures irregularly distributed. Mesosternal keel mainly yellow; metasternum castaneous. Legs yellow; femora with brown freckling, tibiae with brown blotches.

[^11]Abdomen: Venter tan, with dense dark-brown freckling except midline infuscated; anterior margins of sternites and angles dark shiny brown.
Genitalia: Posterolateral angles of pygophore subtruncate in ventral view; median excavation of ventral rim rectangular, lateral borders incrassate-carinate in ventral view (Fig. 5). Diaphragm process oblique at dorsal border of pygophore, projecting about one-third distance from dorsal border to base of paramere. Paramere with percurrent carinae (Figs. 4, 10). Posterior margin of basal process of proctiger bisinuate in dorsal view. Females unknown.
Types: Holotype: male, labeled: (a) BRAZIL, Minas Gerais, Laisance, VIII-1934, E. Dias coll., em ninho de ave, ex-coll. Costa Lima. Deposited MCNZ.
Etymology: This species is dedicated to the late Dr. Angelo da Costa Lima in recognition of his great contributions to entomology in Brazil.
Remarks: This species, along with $P$. peruvianus described below, has the humeri acute, but not cornute. It is distinguished from $P$. peruvianus by having proportionately smaller eyes and the juga longer than the tylus.

## Pseudevoplitus peruvianus, new species

(Figs. 3, 8, 9, 12, 20)
Description: Elongate, ovate, dorso-ventrally depressed with prominent humeral angles. Dorsal color mottled tan.
Male: Measurements. Length of head 2.35; anteocular length 1.21 ; width of head 3.02; width between eyes 1.61 ; width between ocelli 0.54 ; antennal segment I 1.0 , II 2.18, III 2.58, IV and V missing; pronotal length 3.78 ; width across humeri 7.22 (without spines), 8.82 (with spines); scutellar length 5.67 ; basal width 4.45 ; total length 13.86; width across third abdominal segment 7.30 .
Head: Yellow-tan dorsally with scattered reddish punctures. Juga and tylus equal in length; juga slightly convergent apically, apices obtuse, lateral margins dark brown, mildly reflexed (Fig. 3). Width across eyes about one-third greater than length of head. Eyes large; diameter about equal to width of head at anterior one-third. Ocelli large, each separated from adjacent eye by diameter of ocellus. Anterior border of bucculae moderately convex in lateral view. Rostrum attaining apex of abdominal sternite IV in repose; segment III more than twice length of IV. Antennal segment I clearly exceeding apex of head; segment IV longest, approximately $1.4 \times$ length of V. Thorax: Pronotum tan with many reddish-brown, irregularly disposed punctures; narrow reddish-brown band uniting bases of cicatrices. Humeri acutely produced, apices curving posteriorad; antero-lateral pronotal margins irregularly crenulate on anterior half (Fig. 3). Scutellum yellow-tan with reddish-brown punctures on disc and small, irregular, dull brown blotches towards margins; apex acute. Hemelytra yellow-tan with dark brown infuscation over most of surface. Mesosternal keel yellow. Metasternum yellow with black blotches laterally. Evaporatorium yellow with brown freckling. Legs yellow with reddish-brown blotches.
Abdomen: Venter tan with dark brown freckling, denser laterally; midline, anterior margins of sternites and angles dark, shiny brown. Laterotergites yellow with reddishbrown freckling.
Genitalia: Posterolateral angles of pygophore subtruncate in ventral view (Fig. 9). Outline of diaphragm process in a triangular projection at dorsal border of pygophore,
projecting halfway from dorsal border to base of paramere. Posterior margin of basal process of proctiger subtruncate, notched medially in dorsal view (Figs. 8, 12).
Female: Measurements. Length of head 2.52; anteocular length 1.51 ; width of head 3.27; width between eyes 1.51 ; width between ocelli 0.67 ; antennal segment I 1.34, II 1.93, III 2.77, IV 3.36, V 2.68; pronotal length 4.03; width across humeri 8.23 (without spines), 10.08 (with spines); scutellar length 6.72 ; basal width 4.87 ; total length 16.29 ; width across third abdominal segment 8.40.
Genitalia: Laterotergites yellow with reddish-brown freckling, as well as anterior half of gonocoxites 8 ; posterior half of gonocoxites 8 dark brown. Gonocoxites 8 about as long as wide; thinly carinate sutural borders parallel for three-fourths length basally, distal fourth arcuately divergent; posterior borders truncate, parallel to transverse band uniting dorsally laterotergites 8 . Spiracles of laterotergites 8 hidden. Gonocoxites 9 bilaterally feebly tumescent, posterior border bilobate.
Types: Holotype: male, labeled: (a) PERU, Iquitos, III-14-1969, B. K. Dozier, L. H. Rolston Coll. Deposited AMNH.
Paratypes: One male, one female, labeled: (a) PERU, Avispa, X-10-1962, L. Pena coll. Deposited AMNH.
Etymology: peruvianus, latinized, "of Peru."
Remarks: This species can be separated from P. costalimai by the tylus and juga being of equal length, and the large eyes, which are as wide as the head at anterior one-third.

Pseudevoplitus vittatus, new species
(Figs. 1, 13-15, 21)
Description: Elongate-oval, dorso-ventrally depressed with pronotum somewhat gibbous and pronotal humeri strongly produced as cornute spines. Dorsal surface matte, tan, with dark brown longitudinal mesial vitta on pronotum and scutellum (Fig. 1). Male: Measurements. Length of head 2.68; anteocular length 1.68 ; width of head 3.52; width between eyes 1.68 ; width between ocelli 0.84 ; antennal segment I 1.17, II 2.52 , III 2.85 , IV 3.27, V 2.35 ; pronotal length 3.86 ; width across humeri 7.72 (without spines), 10.75 (with spines); scutellar length 5.79 ; basal width 4.53 ; total length 15.45 ; width across third abdominal segment 7.89 .
Head: Yellow-tan dorsally with irregularly disposed reddish-brown punctures. Tylus and juga of equal length, apices of juga slightly convergent; lateral margins darkbrown and mildly reflexed. Ocelli large, distance from ocellus to eye subequal to ocellar diameter. Anterior border of bucculae nearly straight in lateral view. Rostrum attaining apex of abdominal sternite V; segment III longest, nearly $2 \times$ length of segment IV. Antennal segment I almost attaining apex of head, segment IV longest, about $1.4 \times$ length of segment $V$.
Thorax: Pronotum yellow-tan with humeral angles and irregular central quadrate spot dark fuscous; surface with many dark brown punctures tending to be contiguous. Posterior margins of cicatrices united by thin, sinuate, dark-castaneous line. Humeral angles strongly produced as cornute spines. Anterolateral pronotal margins with anterior half irregularly rugose, subtuberculate. Scutellum yellow-tan laterally, darkly infuscated mesially; lateral angles and apex dark brown; apex acute. Hemelytra yellow with many contiguous dark-brown punctures. Mesosternal keel yellow; elevated metasternum dark shiny brown. Legs yellow with dark brown blotches.

Abdomen: Venter yellow-tan with vitta on midline, posterior angles and anterior margin of each sternite dark, shiny brown. Laterotergites yellow-tan with scattered brown freckling and irregular blotch at posterior margins.
Genitalia: Posterolateral angles of pygophore acute in ventral view, bearing minute spine just dorsad of each angle (Figs. 14, 15), ventral rim incrassate each side of median excavation. Outline of diaphragm process in a quadrangular projection at dorsal border of pygophore, projecting nearly to base of paramere; parameres fangshaped. Basal process of proctiger incrassate, bilobate, deeply notched between lobes in dorsal view (Fig. 13).
Female: Measurements. Length of head 3.20; anteocular length 1.84; width of head 3.72; width between eyes 1.88 ; width between ocelli 0.92 ; antennal segment I 1.28 , II-V missing; pronotal length 4.34; width across humeri 7.70 (without spines) 10.75 (with spines); scutellar length 6.64; basal width 5.16 ; total length 16.96 ; width across third abdominal segment 8.44 .
Genitalia: Gonocoxites 8 slightly tumescent, about one-fourth longer than wide; sutural borders parallel for three-fourths length, distal fourth truncate, divergent; external borders slightly reflexed, incrassate, rectilinear; posterior border oblique, truncate, external angles extending posteriorly more than sutural angles (Fig. 21). Posterior border of gonocoxites 9 bilobate. Spiracles of laterotergites 8 partially hidden under gonocoxites 8 .
Types: Holotype: male, labeled: (a) BRAZIL, Rondonia, 62 km SW Ariquemes nr Fazenda Rancho Grande, XII-6/15-1990, D. A. Rider and J. E. Eger, collected at mercury vapor and blacklight. (b) D. A. Rider Collection. Deposited AMNH. Paratype female, labeled: (a) BRAZIL, Amazonas, Manicore, margem do Rio Madeira, VIII-1941, Parko coll. Deposited MCNZ.

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# A NEW SPECIES AND NEW RECORDS OF CYCLOCEPHALA FROM GUATEMALA (COLEOPTERA: MELOLONTHIDAE) 

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#### Abstract

A new Guatemalan species of Cyclocephala is described and modifications to Endrodi's key to the genus are included to allow their identification. New country records for Guatemala are given for C. aequatoria Endrodi, C. alexi Ratcliffe and Delgado, and C. prolongata Arrow.


The American genus Cyclocephala includes more than 250 described species, most of which are distributed in South America (Ratcliffe, 1991). However, many endemic species are present in North and Central America (cf. Endrodi, 1985; Ratcliffe, 1992). Guatemalan species of this genus are poorly studied. Here we describe a new species and record for the first time three species of this genus for Guatemala.

## Cyclocephala batesi, new species

(Figs. 1-3)
Type material. Holotype male, labeled: "GUATEMALA: Zacapa, La Unión, 10-V1992, Alt. 1,300 m, bosque nuboso, luz H. A. Castañeda, col." Allotype female and one female paratype labeled as holotype. Holo and Allotype deposited at the Universidad del Valle de Guatemala (Guatemala City), paratype deposited in collection of Brett C. Ratcliffe (Lincoln, Nebraska).
Description. Holotype male. Total length 14.5 mm ; maximum width (to middle of elytra) 7.4 mm . Color testaceous, except for fuscous posterior middle of frons, vertex, two large spots on pronotum and three small spots on each elytron (Fig. 1). Dorsum glabrous, with scattered, minute setae on apex of elytra only. Clypeus subtapezoidal, sides convergent, apex distinctly emarginate with front angles rounded and feebly reflexed; clypeal surface and frons finely reticulated; clypeus with dense and mediumsized punctures that become sparser and smaller towards frons and vertex. Interocular width equals 3.3 transverse eye diameters. Antenna 10-jointed, club shorter than segments 2-7. Pronotum with posterior angles evenly rounded, base unmargined; pronotal surface with punctures dense and larger than those of clypeus, punctures sparser and smaller near mid-line. Elytra with larger punctures than those of pronotum, intermixed with minute punctures; rows discernible. Pygidium evenly convex, disc with minute and medium-sized punctures, sides rugopunctate, surface with small setae, setae denser on sides. Protibiae tridentate, basal tooth smaller than apical ones and slightly more removed from median tooth than median tooth is from apical;


Figs. 1-3. Cyclocephala batesi n. sp., holotype. 1. Dorsal pattern. 2. Caudal view of parameres. 3. Lateral view of parameres. $\mathrm{Bar}=1 \mathrm{~mm}$.
protarsal inner claw finely split just before apex; meso- and metatarsi only slightly longer than respective tibiae. Genitalia with parameres short and slightly convergent to apex (Figs. 2-3).

Allotype female. Total length 14.3 mm ; maximum width (about at the posterior third of elytra) 7.7 mm . As holotype except in the following respects: pronotal spots larger and partially coalescing at anterior third; surface of clypeus and frons not reticulated; clypeal punctation denser and deeper; elytra with lateral margin distinctly expanded behind middle; pygidium flatter, glabrous, and with sparse, small punctures that become slightly larger and denser at sides; protibiae with basal tooth larger and with teeth equidistant; protarsal inner claw not enlarged; meso- and metatarsi slightly shorter than respective tibiae and a little stouter.
Type locality. La Unión, Zacapa, Guatemala.


#### Abstract

Etymology. Named after the eminent entomologist Henry Walter Bates (1825-1892), in recognition of his many contributions to the knowledge of the Neotropical insects. Remarks. In Endrodi's (1985) key to species of Cyclocephala, this species will key only as far as couplets 291/292 (male key) and 119/120 (female key) where neither choice properly describes the character states present in C. batesi. Therefore, we add the new couplets $290 \mathrm{a} / 290 \mathrm{~b}$ and $118 \mathrm{a} / 118 \mathrm{~b}$ to the keys as follows:


Males:
290(285) Disc of pronotum strongly punctate, more strongly so (or rarely finer than frons).
290a(290b) Each elytron with three spots. Pygidium with short setae, setae denser at sides. Parameres short, without preapical tooth on outer side. Length 14-15 mm. Guatemala ............. batesi Delgado and Castañeda
290b(290a) Each elytron with four or six spots. Pygidium glabrous. Parameres long or with preapical tooth on outer side.
291(292) Pronotum with two longitudinal ................................. etc.
Females:
118(113) Surface bare or at most with a few very short setae on apical half of elytra. Pygidium rarely more distinctly setose.
118a(118b) Each elytron with three spots and without lateral knob. Pygidium scarcely punctate. Length $14-15 \mathrm{~mm}$. Guatemala.
.batesi Delgado and Castañeda
118 b (118a) Each elytron with four or six spots and with lateral knob. Pygidium densely punctate.
119(120) Dilation of lateral margin ......................................... etc.
Distribution. Cyclocephala batesi is only known from the type locality, situated at the region of Trifinio-El Portillo, which includes mountainous frontier areas between Guatemala, Honduras and El Salvador. The discovery of this species helps to support the idea that this region is a zone of high endemism, as suggested by Schuster (1992) on the basis of the distribution of passalid beetles in northern Central America.

## Cyclocephala aequatoria Endrodi

This species was previously known from Mexico and Ecuador (Endrodi, 1985). The following specimens represent a new country record: Guatemala, Alta Verapaz, Panzós, Finca Pueblo Viejo, 14-VI-1989, Alt. 10 m , luz, E. Cano, col.(2 females); same data but 16-VI-1989 ( 1 male); same data but 24-VI-1989 ( 3 males, 5 females); same data but 30-VI-1990 ( 3 females).

## Cyclocephala alexi Ratcliffe and Delgado

This species was described from Mexico and recorded only from the frontier state of Chiapas (Ratcliffe and Delgado, 1990). The following male specimen constitutes a new country record: Guatemala, Baja Verapaz, Purulhá, 21-III-1993, Alt. 1,737 m, A. Morán, col.

## Cyclocephala prolongata Arrow

This species has been recorded from Mexico, Belize, Honduras, Nicaragua, Panama, Colombia and Peru (Ratcliffe, 1992). The following specimens represent a new country record: Guatemala, Alta Verapaz, Panzós, Finca Pueblo Viejo, 14-VI-1989, Alt. 10 m , luz, E. Cano, col. ( 2 females); same data but 16-VI-1989 ( 3 females); same data but 24-VI-1989 ( 1 male, 1 female); same data but 30-VI-1990 (1 male); Guatemala, Izabal, Cerro San Gil, Las Escobas, 24-VI-1993, N. Girón, col. (1 male).

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# CONTRIBUTION TO THE TAXONOMY OF THE PANAMERICAN GENUS FALLCEON (EPHEMEROPTERA: BAETIDAE) 

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#### Abstract

The baetid mayfly genus Fallceon is currently known from Central America, the Greater Antilles, Mexico, and the United States, and includes eleven nominal species: F. alcarrazae, new combination, F. eatoni, F. fortipalpus, new species, F. garcianus, F. longifolius, new combination, F. nikitai, F. planifrons, new combination, F. poeyi, F.quilleri, F. sextus, new combination, and $F$. testudineus, new combination. Larvae belonging to the genus include species with consistent mouthpart morphology but variable with respect to development of a cephalic frontal keel and subapical tarsal claw setae. Caribaetis, originally considered a Cuban subgenus of Baetis, is shown to be a synonym of Fallceon. Baetis sonora is shown to be a synonym of Fallceon quilleri. Fallceon fortipalpus is described from the egg and larval stages. Larvae of $F$. longifolius, $F$. planifrons, and $F$. quilleri are redescribed, and the egg of $F$. quilleri is described for the first time. Fallceon longifolius is reported from continental North America (Mexico) for the first time. A key to the known larvae of Fallceon is provided.


When originally described by Waltz and McCafferty (1987), the genus Fallceon included F. quilleri (Dodds) (type species) from Colorado (USA), F. eatoni (Kimmins) from Sonora (Mexico), F. buenoi (Allen) from San Luis Potosí (Mexico), and F. byblis (Allen and Murvosh) from Baja California Norte (Mexico). Later, McCafferty and Waltz (1990) added F. garcianus (Traver) from Puerto Rico and F. poeyi (Eaton) from Cuba, and synonymized $F$. buenoi, $F$. byblis, and $F$. eatoni with $F$. quilleri. All of the above species had been previously included in the genus Baetis Leach. McCafferty et al. (1992), in their study of the biogeography of the Panamerican mayfly genera, showed that the historical affinities of Fallceon were Neotropical. Kluge (1992a, b) described an additional five species from Cuba under the genus Baetis that have proven to be Fallceon (see below). More recently, McCafferty and LugoOrtiz (1994) studied the syntypes of $F$. poeyi, and reconfirmed McCafferty and Waltz's (1990) placement of this species under Fallceon. In addition, McCafferty and LugoOrtiz (1994) showed that Cuban material identified by Kluge (1992b) as F. poeyi was actually a distinct new species, F. nikitai McCafferty and Lugo-Ortiz, and they reinstated $F$. eatoni as a valid species.

In the present study, we provide new information applicable to Fallceon resulting from our study of new collections of larvae from Central America, the Greater Antilles, Mexico, and the United States. Although not a comprehensive revision of Fallceon, we do include here a discussion of the genus, the description of a new species, and larval redescriptions of certain species, and synoptic discussions of all species known as larvae. In addition, we provide a first key to species based on larvae. Institutions housing the material examined in this study and their abbreviations are
as follows: California Academy of Sciences, San Francisco (CAS); Colorado State University, Fort Collins (CSU); Cornell University, Ithaca, New York (CU); Florida A\&M University, Tallahassee (FAMU); Illinois Natural History Survey, Champaign (INHS); Instituto de Ecología, A. C., Veracruz, Mexico (IEAC); and the Purdue Entomological Research Collection, West Lafayette, Indiana (PERC).

## SYSTEMATICS

## Fallceon Waltz and McCafferty

Fallceon Waltz and McCafferty, 1987:668.
Baetis (Caribaetis) Kluge, 1992a:13. New synonymy.
Baetis (Fallceon) Kluge, 1992b:38.
Waltz and McCafferty (1987) erected the genus Fallceon to incorporate those species previously included in Baetis s. l. that lacked a villopore, had segment 2 of the labial palp poorly developed, had at least the right mandible with a tuft of setae between the prostheca and molar, and possessed a distinct costal hook in the hindwing. Kluge (1992a) erected the subgenus Caribaetis (within Baetis s. 1.) to include species that lacked a villopore, did not possess a frontal keel between the antennal bases, had segment 2 of the labial palp poorly developed, possessed a tuft of setae between the prostheca and molar of each mandible, had unpaired subapical setae on the tarsal claws, and had a distinct hook in the costal process of the hindwing. Kluge (1992b) considered Fallceon to be a subgenus of Baetis, and proposed that its larvae were separable from those of Caribaetis by the presence of a frontal keel between the antennal bases and the lack of unpaired subapical setae on the tarsal claws. Kluge (1992b), however, did not provide any characters to separate the adults of Fallceon from those of Caribaetis.

As has been pointed out by Waltz and McCafferty (1987) and McCafferty and Waltz (1990) the presence of the villopore is indicative of a monophyletic group comprised of Acentrella Bengtsson, Baetiella Uéno, Baetis s.s., Barbaetis Waltz and McCafferty, Heterocloeon McDunnough, Liebebiella Waltz and McCafferty, and Platybaetis Müller-Liebenau. To this list can be added the recently recognized genera Gratia Thomas and Labiobaetis Novikova and Kluge (see McCafferty and Waltz, 1995). The absence of the villopore in Fallceon and Kluge's Caribaetis clearly separates them from that lineage.

The presence or absence of a frontal keel on the larval head and unpaired subapical setae on the larval tarsal claws are variable among species of other baetid genera, and we do not consider these characters to be of generic significance. This and the fact that there are no significant differences in the mouthparts of the larvae classified as Caribaetis do not support the recognition of Caribaetis as a separate genus. The presence of a distinct costal hook in the hindwings of species originally placed under Caribaetis further indicates that Caribaetis is synonymous with Fallceon.

## Fallceon alcarrazae (Kluge), New Combination

Baetis alcarrazae Kluge, 1992a: 18 (egg, larva, male and female subimagos, male and female adults).


1


2


3


Figs. 1-4. Fallceon spp., adults. 1. F. quilleri, forewing. 2. F. sp., hindwing (redrawn from Edmunds et al., 1976). 3. F. eatoni, hindwing (redrawn from Kimmins, 1934). 4. F. eatoni, male genitalia (modified from Kimmins, 1934).

Based on Kluge's (1992a) description and figures of this Cuban species, its larvae are very similar to those of $F$. planifrons (see below). Kluge (1992a, b) separates the two species on the basis of color and size differences and number of tergal scales and angulate scale bases. Color and size differences are generally unreliable for species discrimination in Fallceon, but we consider the size and number of tergal scale bases (both of which are smaller and less abundant in $F$. alcarrazae than in $F$. planifrons) to be reliable characters to separate these two species.

## Fallceon fortipalpus Lugo-Ortiz and McCafferty, new species

Larva. Body length: 5.2-5.5 mm; caudal filaments: unknown. Head: Coloration brown. Antennae brown; very fine, simple setae on scapes and pedicels. Frontal keel present (Fig. 5). Labrum (Fig. 6) sclerotized posterolaterally; anterior margin round, with deep medial emargination; submedial and two or three simple submarginal setae present; intermediate simple seta near center of labrum; marginal setae weakly branched; numerous fine, simple setae scattered dorsally, more abundant on midposterior region. Right mandible 3 (1) +3 denticles; tuft of simple setae between postheca and molar; long, simple seta distally on molar. Left mandible $3+3$ denticles; tuft of simple setae absent between prostheca and molar; triangular process at base of molar. Maxillae robust; palps subequal to galealaciniae; palp segment 1 short; segments 2 and 3 subequal in length, with numerous fine, simple setae; five of six long, simple setae at base of each galealacinia. Labium (Fig. 7) elongate and robust; palp segment 1 long and robust; segment 2 subequal to segment 1 , with six simple setae dorsally; segment 3 almost half as long as segment 2 , with numerous simple setae on surface, not expanded; glossae long and narrow, with $10-11$ and seven to eight simple setae medially and laterally, respectively; paraglossae long and narrow, with two distal rows of simple setae and four to five simple setae dorsally. Thorax: Nota brown, without distinct pattern. Sterna medium brown. Legs pale brown, robust;


Figs. 5-8. Fallceon fortipalpus, larva. 5. Frontal keel (top). 6. Labrum (dorsal). 7. Labium (left-ventral; right-dorsal). 8. Paraproct.
femora dorsally with 14-15 long, robust, simple setae, distal two almost contiguous, with very fine, simple setae between long, robust, simple setae, and ventrally with numerous robust, simple setae and fine, simple setae, shorter than those on dorsal margin; tibiae with numerous robust, simple setae ventrally and dorsally, those on dorsal margin longer and more robust, with three robust, simple setae dorsodistally and two robust, simple setae ventrodistally; tarsi with long, fine simple setae dorsally and 19-20 long, simple setae ventrally, tarsal claws with 13-14 denticles. Abdomen: Color brown, without distinct pattern. Very faint dorsal medial line on terga 2-7; terga 8-9 pale posteriorly; tergum 10 pale on anterior margin. Sterna medium brown. Tergal surfaces with numerous fine, simple setae, scales, and angulate scale bases; posterior margins with sharp spines. Gills platelike, broad, elongate, and richly tracheated; margins serrated, with fine, simple setae between serrations. Paraprocts (Fig. 8) with numerous fine, simple setae and angulate scale bases; 14-16 irregular spines along margin. Bases of caudal filaments light brown.
Egg. Ovoid. Chorion (Fig. 9) with numerous depressions, appearing pitted.
Material examined. Holotype: Female larva, COSTA RICA, San José Prov., Río Parmita Chiquito, rt 12, 6.5 km SW of jct rt 2, $9.703^{\circ} \mathrm{N} / 83.970^{\circ} \mathrm{W}$, IV-10-1987, Holzenthal, Hamilton, and Heyn, deposited at PERC.
Etymology. The specific epithet is an arbitrary combination of letters including the Latin derivations fortis (strong) and palpo (touch). It is an allusion to the strong, robust nature of the labial palps.
Discussion. Fallceon fortipalpus is similar to F. quilleri, and the two may represent sister species. Fallceon fortipalpus differs in the narrowly round anterior margin of the labrum (Fig. 6), the more elongate and robust nature of segment 2 of the labial


Fig. 9. F. fortipalpus. Detail of chorion. (Scale: bar $=1 \mu \mathrm{~m}$ ).
palps (Fig. 7), the narrower glossae and paraglossae (Fig. 7), the less organized spination of the paraprocts (Fig. 8), and the finely pitted chorion of the egg (Fig. 9). The adult of this species remains to be discovered.

Fallceon garcianus (Traver)
Baetis garcianus Traver, 1938:26 (male and female adults). Fallceon garcianus, McCafferty and Waltz, 1990:778.

Traver (1938) described F. garcianus from Puerto Rico. Based on the study of the larval exuviae of the allotype, larvae belonging to F. garcianus appear to differ from those of other species of Fallceon by the presence of two relatively broad brown bands on the caudal filaments. Unfortunately, characters of the mouthparts have been obscured due to the poor conditions in which the specimen was originally slide mounted, and we cannot determine if these characters differ in any significant way from those of other species of Fallceon.
Material examined. Holotype: Male adult, PUERTO RICO, Tanama River, III-131935, J. G. Needham and J. García-Díaz, deposited at CU. Allotype: Female adult (reared from larva), Río Yunez, VI-21-1935, J. García-Díaz, same deposition as holotype. Paratypes, 23 male adults, same data and deposition as holotype; 17 female adults, same data and deposition as allotype.


Figs. 10-15. Fallceon longifolius, larva. 10. Labrum (dorsal). 11. Right mandible. 12. Left mandible. 13. Right maxilla. 14. Labium (left-ventral; right-dorsal). 15. Paraproct.

## Fallceon longifolius (Kluge), New Combination

Baetis longifolius Kluge, 1992b:44 (egg, larva, male and female adults).
Larva. Body length: $6.2-8.0 \mathrm{~mm}$; caudal filaments: unknown. Head: Coloration pale to pale yellow. Antennae pale to pale yellow; few very fine, simple setae on scapes and pedicels. Frontal keel present (Fig. 5). Labrum (Fig. 10) sclerotized posterolaterally; anterior margin subparallel and with deep median emargination; submedial and four or five submarginal simple setae present on each side; intermediate setae absent;
long, fine, simple setae anterolaterally and anteriorly, some setae weakly branched; very short submarginal-anterolateral simple setae present. Right mandible (Fig. 11) $3(1)+3$ denticles; tuft of long, fine, simple setae between prostheca and base of molar; few fine, simple setae distally on molar. Left mandible (Fig. 12) 3 (1) +3 denticles; tuft of fine, long simple setae between prostheca and molar; triangular process at base of molar. Maxillae (Fig. 13) elongate; palps extending beyond galealaciniae; palp segment 1 short; segment 2 almost $2.0 \times$ length of segment 1 ; segment 3 almost $1.5 \times$ length of segment 2 , with very fine, simple setae distally; eight or nine long, simple setae at base of each galealacinia. Labium (Fig. 14) robust; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with five simple setae dorsally; segment 3 basally broad and apically pointed, with many long, robust and long, fine simple setae on surface; glossae broad, tapering distally, with 15-17 long, robust, simple setae medially and 14-16 laterally; paraglossae broad, with three rows of long, robust, simple setae distally. Thorax: Nota pale yellow to pale brown, without distinct pattern. Sterna pale yellow to pale brown. Legs pale yellow to pale brown, long and slender, with small, angulate scale bases scattered over surface; femora with numerous simple setae of intermediate length dorsally and ventrally (some ventral setae weakly branched); tibiae with numerous setae of intermediate length ventrally and dorsally, becoming more abundant distoventrally; tarsi with numerous simple setae of intermediate length ventrally, few dorsally; tarsal claws with 14-16 denticles, increasing in length distally. Abdomen: Color pale yellow to pale brown; shape narrow, elongate. Terga 1-7 darker medially, becoming paler laterally; terga eight-10 pale yellow to pale brown. Sterna pale yellow to pale brown. Tergal surfaces with abundant small, angulate scale bases; posterior margins with sharp, triangular spines and very few simple setae. Gills platelike, very narrow, elongate; gills 3-6 as long as two abdominal segments or longer; margins weakly serrated; tracheation variable. Paraprocts (Fig. 15) with numerous small, angulate scale bases on surface and numerous small, slender spines along margin. Caudal filaments pale yellow to pale brown.
Material examined. Four larvae, MEXICO, Hidalgo, Zacualtipán, pine-oak forest, 2,000 m, XI-13-1985, R. Novelo, deposited at IEAC and PERC.
Discussion. Kluge (1992b) described F. longifolius from southeastern Cuba. Our study of larvae of this species has allowed the comprehensive redescription given above, and our Mexican record significantly extends its known range outside the Greater Antilles into the mainland, indicating that it may be more widespread in the Caribbean and along the Gulf Coast of Mexico. Although F. longifolius can be easily differentiated from other members of the genus in the larval stages, we found additional important structural characters not recognized by Kluge (1992b). These include the subparallel anterior margin of the labrum (Fig. 10), the number of denticles of each mandible (Figs. 11-12), the elongate nature of the maxillae (Fig. 13), and the small size, shape, and number of spines of the paraprocts (Fig. 15). Adults apparently lack reliable characters for separating them from most other members of Fallceon.

McCafferty and Lugo-Ortiz (1994) pointed out that Kluge's (1992b) determination of one of Eaton's syntypes of $F$. poeyi as $F$. longifolius was in all probability incorrect due to extreme size differences between the larvae of $F$. longifolius and that particular specimen. Furthermore, from the poor conditions of that syntype, including its lack of genitalia, it is impossible to identify it to a precise species, and, therefore, it should be regarded as Fallceon sp. (McCafferty and Lugo-Ortiz, 1994).

Fallceon longifolius is the only species of the genus presently known from both the mainland of North America and a Caribbean island. The island in this case is Cuba, where seven species of Fallceon are currently recognized. This leads us to hypothesize that $F$. longifolius is a founder species that perhaps was ancestral to the Cuban species; or, on the other hand, Cuba may have been the origin of Fallceon, and F. longifolius represents its link to North America.

## Fallceon nikitai McCafferty and Lugo-Ortiz

Baetis poeyi, Kluge, 1992b:40 (misidentification; egg, larva, male and female subimagos, male and female adults).
Fallceon nikitai McCafferty and Lugo-Ortiz, 1994.
Based on the study of the syntypes of Baetis poeyi, McCafferty and Lugo-Ortiz (1994) determined that Kluge's (1992b) reared material represented another distinct species within Fallceon, and assigned it the name F. nikitai. Eaton's syntypes lack the hooked costal process of the hindwing, whereas Kluge's material possessed it (McCafferty and Lugo-Ortiz, 1994). Larvae of F. nikitai are difficult to characterize based on available descriptions. Kluge (1992b) indicated that they could be separated from other larvae of Fallceon by the shape of the gills, which are wider medially [see Kluge, 1992b: fig. 1(7-13)].

## Fallceon planifrons (Kluge), New Combination

Baetis planifrons Kluge, 1992a:15 (egg, larva, male and female adults).
Larva. Body length: $4.0-4.5 \mathrm{~mm}$; caudal filaments: unknown. Head: Coloration pale yellow to pale brown. Antennae pale yellow to pale brown. Frontal keel absent. Labrum (Fig. 16) sclerotized posterolaterally, anterior margin rounded, with deep median emargination; submedial and two to three submarginal simple setae on each side; intermediate setae absent; long, fine, simple setae anterolaterally and anteriorly, those on anterolateral margin longer and often branched. Right mandible (Fig. 17) $3+1+4$ denticles; tuft of simple setae between prostheca and molar; base of incisors with seven to eight simple setae; distal end of molar with one long, simple seta. Left mandible (Fig. 18) $3+1+3$ denticles; almost inconspicuous tuft of simple setae between incisors and molar; blunt triangular process at base of molar; short, stout, simple setae at base of triangular process and molar. (Very small apical denticle sometimes present in both mandibles.) Maxillae (Fig. 19) short and robust; maxillary palps 3 segmented, subequal to galealaciniae; five or six fine, simple setae at base of galealaciniae; palp segment 1 short; segments 2 and 3 subequal in length, with scattered fine, simple setae. Labium (Fig. 20) long and robust; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with four to five simple setae dorsally; segment 3 apically rounded, with many setae of various lengths on surface; glossae narrow, tapering distally, with 13-15 simple setae medially and eight to nine simple setae laterally; paraglossae basally broad, tapering distally, with two apical rows of simple setae. Thorax: Nota pale yellow to pale brown. Pronotum often with very faint medial pale markings. Sterna pale yellow. Legs pale yellow, slender, with few and almost inconspicuous angulate scale bases on surface; femora dorsally with numerous long, simple setae (more abundant basally), ventrally with short, stout


Figs. 16-22. Fallceon planifrons. 16. Labrum (dorsal). 17. Right mandible. 18. Left mandible. 19. Right maxilla. 20. Labium (left-ventral; right-dorsal). 21. Tergal surface (redrawn from Kluge, 1992a). 22. Paraproct.
setae, and medial large, brown macula on anterior face (macula sometimes faded on forelegs); tibiae with short, stout, simple setae ventrally, dorsal margin bare; tarsi with seven to nine short, stout, simple setae ventrally, dorsal margin bare; tarsal claws with $9-10$ denticles, one subapical seta present. Abdomen: Color pale yellow to pale brown. Terga 1-2 pale brown (tergum 2 often with faint submedian round spots); terga 3-5 pale brown, with pale submedian spots; terga 6-7 pale brown; tergum 8 pale yellow, anteriorly pale brown; terga $9-10$ pale yellow. Sterna pale yellow.

Tergal surfaces (Fig. 21) with abundant large angulate scale bases and scattered fine, simple setae; posterior margins with sharp triangular spines. Gills platelike, broad, with numerous serrations and fine, simple setae along margin. Paraprocts (Fig. 22) with scattered small angulate scale bases and fine, simple setae; spination irregular, distal spines larger than those on lateral margin. Caudal filaments pale yellow to pale brown.
Material examined. Four larvae, CUBA, Granma Prov., Río Buey, Minas de Buey, nr Yara, no date, deposited at FAMU and PERC; two larvae, Granma Prov., La Güira, Yateras, XI-13-1964, deposited at FAMU; two larvae, Matanzas Prov., Río Limonar, X-18-1964, deposited at FAMU; one larva, Santiago de Cuba Prov., Río Jojo, Cajabalo, XI-14-1964, deposited at FAMU; one larva, unknown province, San Vicente, X-31-1964, deposited at FAMU.
Discussion. Kluge (1992a) described F. planifrons from central and western Cuba. Our study of larvae allowed the more comprehensive redescription given above, and extends the known range of the species towards the southeastern part of the island. Kluge (1992a) designated this species as the type species of his Caribaetis; however, it clearly belongs to Fallceon (in discussion under Fallceon, above). The larvae of $F$. planifrons and $F$. alcarrazae are very similar. Kluge (1992a) separated them on the basis of abdominal coloration and the number and size of scales and angulate scale bases on the terga (Fig. 21).

## Fallceon poeyi (Eaton)

Centroptilum poeyi Eaton, 1885:179 (male adult).
Baetis poeyi, Edmunds, 1974:289.
Fallceon poeyi, McCafferty and Waltz, 1990:778.
Baetis (Fallceon) poeyi, Kluge, 1992b:40.
Fallceon poeyi, McCafferty and Lugo-Ortiz, 1994.
Fallceon poeyi has had a somewhat confused taxonomic history. Eaton (1885) originally described the species under Centroptilum Eaton based on the elongate shape of the hindwings. Edmunds (1974) transferred it to Baetis on the basis of the presence of double marginal intercalaries in the forewings. McCafferty and Waltz (1990) recognized that it belonged to Fallceon. Kluge (1992b) treated it under Baetis. More recently, McCafferty and Lugo-Ortiz (1994) studied Eaton's syntypes of C. poeyi. Three of the four, including the specimen designated as the lectotype by Kluge (1992b), do not possess the hooked costal process in the hindwings. Their hindwings agree with Eaton's (1885) figure of such, thus confirming his species concept, and disallowing his fourth syntype since it possessed a hooked costal process (see also discussion under $F$. longifolius, above). Unfortunately, the male types of $F$. poeyi are in such poor condition that their genitalia cannot be adequately characterized. McCafferty and Lugo-Ortiz (1994) determined that Kluge's recently collected material identified as $F$. poeyi was in fact misidentified (see discussion under $F$. nikitai, above).

## Fallceon quilleri (Dodds)

Baetis quilleri Dodds, 1923:112 (female adult).
Baetis endymion Traver, 1935:686 (male adult).
Baetis erebus Traver, 1935:687.


Figs. 23-28. Fallceon quilleri. 23. Labrum (dorsal). 24. Right mandible. 25. Left mandible. 26. Right maxilla. 27. Labium (left ventral; right-dorsal). 28. Paraproct.

Baetis leechi Day, 1954:29.
Baetis cleptis Burks, 1954:130.
Baetis quilleri, Morihara and McCafferty, 1979:215 (larva).
Baetis byblis Allen and Murvosh, 1983:427.
Baetis buenoi Allen, 1985:332.
Fallceon byblis, McCafferty and Waltz, 1990:778.
Fallceon buenoi, McCafferty and Waltz, 1990:778.
Fallceon quilleri, Waltz and McCafferty, 1987:668.
Baetis sonora Allen and Murvosh, 1987:1096. New synonymy.


Fig. 29. Fallceon quilleri. Egg. (Scale: bar $=10 \mu \mathrm{~m}$ ).

Larva. Body length: 4.0-6.5 mm; caudal filaments: $4.0-5.0 \mathrm{~mm}$.
Head: Coloration pale brown to medium brown, with highly variable pattern. Antennae pale yellow to pale brown; few short, stout and fine, simple setae on scapes; short, fine, simple setae on pedicels, rarely with short, robust, simple setae. Frontal keel present (Fig. 5). Labrum (Fig. 23) sclerotized posterolaterally; anterior margin broadly rounded and with deep anteromedian emargination; submedial and two to five submarginal simple setae present on each side; intermediate setae absent; long, fine, simple setae anterolaterally and anteriorly, some weakly branched setae present. Right mandible (Fig. 24) 3 (1) +4 denticles; row of fine, simple setae at base of incisors; tuft of simple setae between prostheca and molar. Left mandible (Fig. 25) $3(1)+1+3$ denticles; tuft of simple setae between prostheca and molar present or absent. Maxillae (Fig. 26) robust; palps subequal or extending beyond galealaciniae; palp segment 1 very short; segments 2 and 3 subequal in length, with scattered fine, simple setae on surface; four or five simple setae at base of galealaciniae. Labium (Fig. 27) robust; palp segment 1 subequal to segments 2 and 3 combined; segment 2 with four to six simple setae dorsally; segment 3 basally broad and apically pointed, with many simple setae on surface; glossae broad, tapering distally, with 15-17 simple setae medially and 14-16 simple setae laterally; paraglossae broad, with two rows of simple setae distally and five simple setae dorsally. Thorax: Nota pale brown to medium brown. Pronotum usually with distinct pattern [see Morihara and McCafferty (1979): Fig. 37c]. Sterna pale brown to medium brown. Legs pale brown to medium brown, robust, with few, almost inconspicuous angulate scale bases on surface; femora
with 25-30 long, simple setae dorsally and numerous simple setae ventrally (those on ventral margin shorter than those on dorsal margin); tibiae with numerous short, simple setae dorsally and ventrally, becoming longer and more abundant distoventrally; tarsi with 20-25 long, simple setae ventrally, dorsal margin bare; tarsal claws with 10-13 denticles. Abdomen: Color pale brown to medium brown, with highly variable patterns. Sterna pale brown to medium brown. Tergal surfaces with fine, simple setae, scales, and angulate scale bases; posterior margins with sharp, triangular spines. Gills platelike, variable in length and width; margins serrated, with fine, simple setae; tracheation variable. Paraprocts (Fig. 28) with angulate scale bases over surface; numerous sharp spines along margin. Caudal filaments pale to pale brown; terminal filament $0.5-0.8 \times$ length of cerci.
Egg. Ovoid; chorion with numerous small round protuberances (Fig. 29).
Material examined. Baetis cleptis. Holotype: Male adult, USA, Illinois, Detroit, IX-15-1939, Ross and Mohr, deposited at the INHS. Paratype: same data and deposition as holotype. Baetis endymion. Holotype: Male adult, USA, Oklahoma, Johnston Co., III-19-1932, A. Sandoz, deposited in CU. Paratypes, 16 males, same data and deposition as holotype. Baetis erebus. Holotype: Male adult, USA, Arizona, Santa Catalina Mountains, Bear Canyon, V-3-1931, L. P. Wehrle, deposited in CU. Allotype: Female adult, USA, Arizona, I-15-1921, same deposition as holotype. Paratypes: Male adult, same data and deposition as holotype; female adult, same data and deposition as allotype. Baetis sonora. Holotype: Female larva, MEXICO, Sonora Sta., Río Cuchujaqui, 15.6 km SE Alamos, I-16-1983, R. K. Allen and C. M. Murvosh, deposited at CAS. Additional material examined: One male adult, HONDURAS, 5 mi W of Jícaro Galán, VII-9-1965, P. J. Spangler, deposited at PERC; three larvae, COSTA RICA, Río Tenorio at Finca La Pacífica, E of Panamerican Hwy, II-8-11-1969, W. P. McCafferty, deposited at PERC; three male adults, MEXICO, Chiapas Sta., Arriaga, VIII-22-1965. P. J. Spangler, deposited at PERC; four larvae, MEXICO, Chihuahua Sta., small stream S of Pacheco, I-22-1987, B. C. Kondratieff; one larva, MEXICO, Chihuahua Sta., Río Piedras Verdes at Colonia Pacheco, I-22-1987, B. C. Kondratieff, deposited at PERC; one larva, MEXICO, Sinaloa Sta., Hwy 15, nr Elota, R. K. Allen and C. M. Murvosh, deposited at PERC; two larvae, USA, Iowa Sta., Story Co., Saper's Mill Park, VIII-8-1991, T. Klubertanz, deposited at PERC.
Discussion. Fallceon quilleri is a widespread species in Central America, Mexico, and the United States (Morihara and McCafferty, 1979; McCafferty, 1985; McCafferty and Waltz, 1990). The species shows extreme variability in size and coloration in the larval stage. Some southwestern populations in the United States are pale brown to yellow in terga 1, 4-5, and 8-10 (see Allen and Murvosh, 1987: fig. 5) and are relatively small $(2.5-3.5 \mathrm{~mm})$. Those populations are typical of those previously assigned to the junior synonym B. sonora. Most midwestern United States, Mexican, and Central American populations show an abdominal color pattern similar to that illustrated by Morihara and McCafferty (1979:fig. 37a) and vary widely in size. Recent collections from streams in Iowa have revealed populations with a pale brown abdomen and a pale mid-dorsal stripe. Despite this variability, the larvae of $F$. quilleri are consistent in labral (Fig. 23) and labial (Fig. 27) morphology and spination of the paraprocts (Fig. 28). Male adults of $F$. quilleri have diagnostic genitalia, shared only by F. eatoni (Fig. 4). These species, however, can be differentiated by the presence
of a distinct costal hook in the hindwings of $F$. quilleri (see also McCafferty and Lugo-Ortiz, 1994). Chorionic sculpturing of the eggs (Fig. 29) suggests that F. quilleri and $F$. fortipalpus may be closely related.

Based on the description of Allen and Murvosh (1987), McCafferty and Waltz (1990) placed B. sonora as a junior synonym of Baetis tricaudatus Dodds. After close examination of the types of B. sonora, however, it's clear that the name is referable to a southwestern variable of $F$. quilleri, as noted above.

## Fallceon sextus Kluge, New Combination

Baetis sextus Kluge, 1992b:45 (egg, larva, male and female adults).
Kluge (1992b) described $F$. sextus from southeastern Cuba only. It appears to be very closely related to $F$. nikitai, and it shows very minor differences with that species. According to Kluge (1992b), larvae belonging to $F$. sextus can be differentiated from those of $F$. nikitai by the shape of the gills, which in $F$. sextus are wider at the distal end.

## Fallceon testudineus (Kluge), New Combination

Baetis testudineus Kluge, 1992b:45 (egg, larva, female subimago).
Fallceon testudineus is known to occur in southeastern Cuba only (Kluge, 1992b). According to Kluge (1992b), it appears to be related to F. longifolius. It differs from that species in the shorter gills and apically narrowed paraglossae. Its larvae differ from those of $F$. quilleri in their narrow glossae and paraglossae.

## KEY TO THE KNOWN LARVAE OF FALLCEON

1 Frontal keel present (Fig. 5) ..... 2
1' Frontal keel absent ..... 7
2 Abdominal gills 3-6 at least as long as two abdominal segments; paraprocts with numerous small marginal spines (Fig. 15) longifolius
$2^{\prime}$ Abdominal gills 3-6 at most as long one and a half abdominal segments; paraprocts with relatively large marginal spines (Figs. 8, 22, and 28) ..... 3
3 Paraglossae narrow and pointed apically ..... testudineus
$3^{\prime}$ Paraglossae broad and rounded apically (Figs. 7, 27) ..... 4
4 Labrum somewhat pointed anteriorly, with branched setae dorsally (Fig. 6); glossae and paraglossae elongate (Fig. 7) fortipalpus
$4^{\prime}$ Labrum rounded anteriorly, without branched setae dorsally (Fig. 23); glossae and paraglossae broad (Fig. 27) ..... 5
5 Distributed in North and Central America ..... quilleri
$5^{\prime}$ Distributed in Cuba ..... 6
6 Abdominal gills widest distally ..... sextus
$6^{\prime}$ Abdominal gills widest medially ..... nikitai
7 Caudal filaments with two broad brown bands; distributed in Puerto Rico .... garcianus
7' Caudal filaments unicolorous; distributed in Cuba ..... 8
8 Scales on terga small and sparse alcarrazae
$8^{\prime}$ Scales on terga large and dense (Fig. 21) ..... planifrons

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# A NEW SPECIES AND NEW RECORD OF CATOGENUS WESTWOOD FROM THE DOMINICAN REPUBLIC (COLEOPTERA: PASSANDRIDAE) 

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#### Abstract

Catogenus slipinskii Thomas, n. sp., is described from the Dominican Republic. It is illustrated and compared with other species of the genus. Catogenus cayman Slipinski is also recorded from the Dominican Republic. These are the first species of Catogenus to be recorded from Hispaniola.


There were 17 species of Catogenus Westwood listed in the recent revision of the genus (Slipinski, 1989), all confined to the New World. Only two species, C. darlingtoni Slipinski and C. cayman Slipinski, were recorded from the Greater Antilles, and those only from Puerto Rico, although species inhabit the Bahamas, the Cayman Islands, and the Virgin Islands (Slipinski, 1989). On a recent trip to the Dominican Republic I discovered a single specimen of an undescribed species in the collection of the Museo Nacional de Historía Natural (MHND) in Santo Domingo. Later I was fortunate to collect a second specimen. The species is described below.

I have also examined a single specimen of C. cayman Slipinski with the following data: ""DOM. REP.: Prv. Pedernales 24 km N Cabo Rojo 1807'N, 71³8'W 09JULY1993, uv light D. Sikes \& R. Rosenfeld." Slipinski (1989) recorded C. cayman from the Cayman Islands, Puerto Rico, and Trinidad.

## Catogenus slipinskii Thomas, new species

Figures 1-3
Diagnosis. The presence of the tubercle on the frons (Fig. 1) is unique among the known species of the genus and is sufficient for identification purposes.
Description. Length, 7.1 mm . Color red-brown; epistome, basal margin of pronotum, and knees piceous.
Head. Transverse, twice as wide as long (length measured from anterior margin of clypeus to occipital groove); admedian grooves absent; frons depressed, with conspicuous median tubercle; epistome over antennal insertions expanded so that anterior margin of head with a "squared-off" appearance; clypeus distinctly separated from frons by a suture and abrupt change of angle, truncate anteriorly, with a median tubercle and lateral impressions; median line not strongly impressed, connecting with depressed area of frons; occipital groove not strongly impressed; lateral carina reaching behind posterior margin of eye and obscurely joined to occipital groove; punctation coarse and dense laterally on frons and occiput, punctures elongate, about the diameter of a facet, separated by $0-1$ diameters; frons sparsely punctate at middle, tubercle densely punctate; antennomeres III-X subequal in length, each submonili-


Fig. 1. Catogenus slipinskii Thomas, n. sp. habitus.


Figs. 2-3. Catogenus slipinskii Thomas, n. sp. 2) aedeagus; 3) paramere, setae omitted.
form, scape 1.14 and pedicel 0.71 times length of flagellar antennomeres; antennomere XI 1.28 times length of flagellar antennomeres; eyes moderate in size, length in dorsal view 0.5 times length of head.
Thorax. Pronotum barely transverse (1:1.04), widest just behind apex, strongly constricted near basal third, width at base 0.73 times width at apex; apical angles obtuse, lateral margin entirely visible from above; punctation dense and coarse on disk except for a median longitudinal impunctate area, punctures larger than on head, elongate; punctation less dense and less coarse anteriorly and laterally. Elytra together 2.35 times longer than combined width, 2.57 times longer than pronotum; lines I-V grooved, VI punctate; humeral carina sharp, complete; intervals slightly convex, each with a single confused row of micropunctures.
Venter. Prosternum heavily punctate laterally, impunctate medially; mesosternum margined with a few punctures just inside marginal lines, medially impunctate and not foveate; groove of abdominal sternite VII slightly angulate in middle.
Genitalia. Male genitalia as in Figures. 2-3.
Types. Holotype male (not dissected), in the Florida State Collection of Arthropods, with the following label data: "DOMINICAN REPUBLIC: Pedernales Prov., 20.5 km N Cabo Rojo 21-V-1992 MCThomas at MV \& UV light"; paratype male (dissected), in MHND, with following label data: "REPUBLICA DOMINICANA: Prov. Bani, Peravia 15-IX-1972 Dominguez \& Reynoso"/"09430."
Variation. The male paratype does not differ in any appreciable way from the holotype.
Etymology. This species is named after S. A. Slipinski, who has done much to advance the systematics of cucujoid Coleoptera.
Biology. Nothing is known about the biology of C. slipinskii except that it is attracted to light at night. Other species of Catogenus for which biological information is available are ectoparasitic as larvae on pupae of Cerambycidae (Dimmock, 1884; Fiske, 1905) and generally the adults are found under the bark of cerambycid infested trees.
Discussion. In Slipinski’s 1989 key, C. slipinskii goes to the second couplet, but does not agree with either choice. This species and C. darlingtoni Slipinski are the only known species of Catogenus with the clypeus set off from the frons by a well-defined groove, but C. slipinskii differs from C. darlingtoni in possession of a frontal tubercle, lack of admedian grooves on the head, humeral carina strongly developed, and mesosternum not foveolate. The frontal structures of the two species may represent convergence.

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# TAXONOMIC NAMES PROPOSED IN THE INSECT ORDER HETEROPTERA BY JOSÉ CANDIDO DE MELO CARVALHO FROM JANUARY 1989 TO JANUARY 1993 

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Abstract. - A list of taxonomic names of Heteroptera proposed by José C. M. Carvalho, alone or in coauthorship, from January 1989 to January 1993, is presented. Included are 59 genusgroup names and 343 species-group names. For each name the original reference is cited and the present depository for holotypes is given. Two species of the genus Dolichomiris (planifrons, uniformis) omitted from the first list (1987) are incorporated here in their alphabetical position.

## CONTENTS

Introduction ..... 481
Family Colobathristidae ..... 482
Family Dipsocoridae ..... 482
Family Miridae ..... 482
Genus-group Names ..... 482
Species-group Names ..... 485
Family Reduviidae ..... 507
Family Tingidae ..... 507
Acknowledgments ..... 508

This is the third list of Carvalho-described taxa in Heteroptera and encompasses the period from January 1989 to January 1993. It contains 59 genus-group names and 347 species-group names. The first list, for the period 1943 to January 1985, containing 254 genera and 1,260 species, was published in the Journal of the New York Entomological Society, 95:121-224 (1987); the second list, for the period from January 1985 to January 1989, with 72 genera and 480 species and subspecies, was published in the same journal, 98:310-346 (1990). The present list continues the practice of including the original citation and, for species and subspecies, the stated holotype data, and institution of holotype deposition.

Incorporated in this list, in their alphabetical positions, are two Dolichomiris species, planifrons and uniformis, published by Eyles and Carvalho (1975) and inadvertently omitted from the first list (1987).

[^12]
## LIST OF NAMES PROPOSED

FAMILY COLOBATHRISTIDAE
Species-group Name
Peruda brasiliana Carvalho \& Costa, 1989
Rev. Brasil. Biol., 49(2):485, figs. 1-9; H ô, Serra dos Carajás, Estado do Pará, Brasil, II, 1988, Roppa e Magno col.; MN.

## FAMILY DIPSOCORIDAE

## Species-group Name

Trichotonannus sulawesicus Carvalho, 1989
Bull. Inst. R. Sci. Nat., 58:185, figs. 1-15; H ô, Sulawesi, Utara, Dumonga Bone National Park, Hogg's Back subcamp, 600 m, 15.XI.1985, Station 005, leg. R. Bosmans \& J. Van Stalle, Lg n. a. 26.977; P 2ôô, 2ㅇํ; IRSN.

## FAMILY MIRIDAE

Genus-group Names
Adcylapocoris Carvalho, 1989
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):80.
Adlopidea Carvalho, 1989
Rev. Brasil. Biol., 49(1):262.
Adnotholops Carvalho, 1990
An. Acad. Brasil. Ci., 62:394.
Alvarengamiris Carvalho, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 6(1):90.
Anolaimus Carvalho, 1990
Rev. Brasil. Biol., 50(2):497.
Blumenaucoris Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1)69.
Bolivarmiris Carvalho, 1989
Rev. Brasil. Biol., 49(2):466.
Catarinea Carvalho \& Costa, 1992
An. Acad. Brasil. Ci., 64(2):193.
Cephaloresthenia Carvalho \& Carpintero, 1992
Revta. Brasil. Zool., 7(1-2): 185.
Clypeocoris Carvalho, 1989
Rev. Brasil. Biol., 49(2):444.
Cordovadisca Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):93.
Cylapocoroides Carvalho, 1989
Rev. Brasil. Biol., 49(2):444.
Cylocorella Carvalho, 1989
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):84.

Cylocorisca Carvalho, 1989
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):86.
Dijocaria Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):34.
Divisotylus Carvalho, 1990
An. Acad. Brasil. Ci., 62(4):409.
Fulviella Carvalho, 1991
An. Acad. Brasil. Ci., 63(4):404.
Fulvioaustrus Carvalho, 1991
An. Acad. Brasil. Ci., 63(4):403.
Ganocapsisca Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):199.
Garganisca Carvalho, 1990
An. Acad. Brasil. Ci., 62(1):75.
Goiastylus Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):44.
Guapimirella Carvalho, 1990
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VII.89, F. Reinboldt; P 2ơ̂, 3i̊q; IBUN.

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AM (Amazonas), Brasil, X.79, M. Alvarenga col.; P 1ठ, 1̊; MN.
Amapacylapus englemanni Carvalho, 1992
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Anolaimus nigrus Carvalho, 1990

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Antias boumilae Carvalho, 1989
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Antias paranaensis Carvalho, 1990
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Antias peruana Carvalho, 1991
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Araucanocoris subandinus Carvalho \& Carpintero, 1991
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Bergmiris minusculus Carvalho \& Carpintero, 1990
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Blumenaucoris catarinensis Carvalho \& Costa, 1992
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Bolivamiris grandis Carvalho, 1989
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Brasiliocarnus goianus Carvalho \& Costa, 1991
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Brooksetta californiana Carvalho, 1990
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Cafayatina inesalti Carvalho \& Carpintero, 1991
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Carijoanus bahiensis Carvalho, 1990
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Carijoanus venezuelanus Carvalho, 1989
Rev. Brasil. Biol., 29(2):468, figs. 19-22; H ठ', Venezuela, Merida, Carbonera, 2.600 m, 8.X.69, J. e Bechyné leg; P 1ठ̊; MEFFY.
Carmelus meridianus Carvalho, 1989
Rev. Brasil. Biol., 49(2):469, fig. 23; H 9 , Santa Cruz de la Cascada, Venezuela, Merida, 10.VII.1979, B. Bechyné leg.; P 1ô; MEFFY.
Carpinteroa patagonica Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1109, figs. 1-5; H ठ, Colorado, Rio Negro, Argentina, XI.46, Carpintero; P 26ồ̂, 40\%̊; CC.

Catarinea plaumanni Carvalho \& Costa, 1992
An. Acad. Brasil. Ci., 64(2):194, fig. 3; H 9, Brasil, Nova Teutonia, Santa Catarina, $27^{\circ} 11^{\prime} \mathrm{N}, 52^{\circ} 23^{\prime} \mathrm{W}$, Nov. 1974, Fritz Plaumann col.; MN.
Chileria colla Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):33, figs 1, 9-12; H ठ, El Alisal, Salta, Argentina, 1.600
M; I.90, Carpintero; P 130ôơ, $112 \not 2 \%$; C.
Chiloxionotus chaquensis Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1110, figs. 6-9; H ô, Resistencia, Chaco, Argentina, XII. 35; CC.

Chiloxionotus guaranianus Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1113, figs. 10-13; H $\ddagger$, Foz do Iguaçu, Paraná, Brasil, 7.XII.66, lampada mercúrio, Dept. Univ. Paraná; P 1ớ; MN.

Chiloxionotus willneri Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1113, figs. 14-17; H ô, Tucuman, 4.300 m , Argentina, XI.64; CC.

Chinamiris acutispinosus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:276, figs. 5, 12, 19, 41, 43, 50-53; H ô, k. A. Mt.
Snowflake, lower slope, 25 Oct.1962, A. E. Eyles; A 9 , P 35ơơ, 36\%̊; NZAC.
Chinamiris aurantiacus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:277, figs. 42, 44, 84-86; H ठ̂, S. D. Stephens I, sweeping,

Chinamiris brachycerus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:280, figs. 3-4, 15, 54-57; H ô, GB, Urewera National
Park, Hiuiarau Range, Putahinu Ridge, $3,840 \mathrm{ft}(1,170 \mathrm{~m})$ on Coprosma, 2 Mar.
1971, A. C. Eyles; A $\ddagger$, P 7 ôô, 3 와; NZAC.
Chinamiris citrinus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:281, figs. 46, 58-60; H 九九, TO, Mt. Reapehu, Iwikau,

Chinamiris cumberi Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:282, figs. 23, 31, 47; H ठ, WI, Paiaka, (Manawatu), R.A.

Chinamiris elongatus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:286, figs. 74-75, 87-89; H ठ̂, WD, Otira, 15 Nov. 1959,

Chinamiris daviesis Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:283, fig. 48; H ô, HB, Puketitiri, Little Bush, 16 Jan. 1986, T. H. \& J. M. Davies; A 9, P of; NZAC.
Chinamiris dracophylloides Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:284, figs. 8, 18, 32, 49, 61-63; H 8, FD, Wilmot Pass, $1,067 \mathrm{~m}$, upper bush edge on Dracophyllum, Manapouri Exped. Jan. 1970, A. C.

Chinamiris fascinans Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:288, figs. 24-25, 33, 76, 90-92; H ơ, SD, Stephens I,
sweeping, Feb. 1971, J. McBurney; A q, P 6ổ̂, 1̊; NZAC.
Chinamiris guttatus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:289, figs. 77, 93-95; H ơ, BR, Lake Rotoiti, 29 Oct.
1964, E. S. Gourlay; A 9, P 3ổ̊, 8̊̊̊; NZAC.

Chinamiris hamus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:290, figs. 78, 96-98; H ô, BR, Lake Rotoiti, 29 Oct. 1964, E. S. Gourlay; A $\$$, P ; NZAC.
Chinamiris indeclivis Eyles \& Carvalho
New Zealand J. Zool., 18:291, figs. 30, 36, 79-80, 99-101; H ô, WN, Packakariki, Queen Elizabeth Park, 11 Nov. 1977, E. Schlinger, A \&, P 37ô̊, 39̊̊; NZAC.
Chinamiris juvans Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:293, figs. 37, 82; H ô, NN, Cobb Reservoir, Trilobite Hut, 820 m, swept in Nothofagus forest, Feb. 1985, J. W. Early; A 9, P 2\%я; NZAC. Chinamiris marmoratus Eyles \& Carvalho, 1991

New Zealand J. Zool., 18:297, figs. 21, 105, 114-117; H ठ̂, NN, Nelson Entomology Division on Coprosoma repens hedge, 3 Nov. 1971, A. C. Eyles; A q, P 5ồ̂, 2̊̊; NZAC.
Chinamiris minutus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:298, figs. 64-66, 106; H ô, FD, Wilmot Pass, 630-800 m, on Coprosma, Manapouroi Exped., Jan. 1970, G. W. Ransay; A \&, P 23ôô, 29\%q; NZAC.
Chinamiris nicuilatus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:300, fig. 108; H ó, WI, Wanganui, Longacre Rd, 27 Jan. 1982, C. F. Butcher; NZAC.
Chinamiris nigrifrons Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:300, figs. 17, 67-69, 109; H đ̂, NN, Mt. Arthur, 1,000-

Chinamiris opacus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:302, figs. 22, 110, 122-125; H ô, RI, Ruhaine Range, Maropea Hut, 1,219 m, on Coprosma, 22 Feb. 1970, G. W. Ramsey; A 9, P 2 ôô, 3와; NZAC.
Chinamiris ovatus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:303, figs. 29, 111, 126-128; H ô, TO, Turangakumu (Napier-Taupo Road), 16 Feb. 1954, R. A. Cumber; A 9, P 9 ôô, 10œ̊; NZAC.
Chinamiris punctatus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:304, figs. 34-35, 112, 129-131; H ô, WD, Franz Josef, $650 \mathrm{ft}(198 \mathrm{~m}), 2$ Nov. 1965, J. I. Townsend; A $\ddagger$, P 10ôઠ́, 10æ\%; NZAC.
Chinamiris quadratus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:305, figs. 9, 20, 113, 132-135; H ठ̂, FD, Hunter Mts., Mt. Burns, 914 m, 9 Jan. 1970, J. I. Townsend; A 9 , P 17ôô, 11 i̊; NZAC.
Chinamiris rufescens Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:307, figs. 27, 39, 70-73, 136; H ô, NN, Mt. Arthur, 1,000-1,524 m, sweeping, 3 Feb. 1982, C. F. Butcher; A \&, P 14ôô, 16와; NZAC. Chinamiris secundus Eyles \& Carvalho, 1991

New Zealand J. Zool., 18:308, fig. 137; K ô, ND, Ngaiotonga, forest sweep, 29 Feb. 1960, R. A. Cumber; A 9 , P 19; NZAC.
Chinamiris testaceus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:309, figs. 26, 38, 145-147; H 九̂, TK, Dawson Falls Road, 823 m, on Olearia arborescens, 21 Oct. 1968, J. S. Dugdale; A 9, P 6ôô, 89̊; NZAC. Chinamiris unicolor Eyles \& Carvalho, 1991

New Zealand J. Zool., 18:310, figs. 28, 40, 139, 148-150; H ô, MC, Arthur's Pass,

Dobson Memorial Walk, sweeping, 8 Feb. 1982, C. F. Butcher; A q, P 21 ôô, 9 9̊̊; NZAC.
Chinamiris virescens Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:311, figs. 1, 6, 140, 151-153; H ô, MC, Sumner, Summit track, on broom, 5 Jan. 1966, A. C. Eyles; A $\ddagger$, P 4ôô, 4ịq; NZAC.
Chinamiris viridicans Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:312, figs. 10-11, 141-142, 154-156; H ô, NN, Roding River, on Carpodeus, 19 Oct. 1965, J. I. Townsend; A $\ddagger$, P 37ô̊, 47 $\ddagger$; NZAC.
Chinamiris whakapapae Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:324, figs. 143, 157-158; H 九̂, TO, Mt. Ruapehu, Whakapapa, 3,700 ft (1,129 m), general beating, 27 Nov. 1965, J. I. Townsend; A \&, P 1ổ̂, 3와; NZAC.
Chinamiris zygotus Eyles \& Carvalho, 1991
New Zealand J. Zool., 18:315, figs. 144, 159-161; H ô, CO, Rock and Pillar Range, Stonehenge Track, 1,280 m, sweeping, 12 Feb. 1986, C. A. Muir; A ¢ , P 1ô, 4̣̊; NZAC.
Chrysodasia jamaicana Carvalho, 1990
Rev. Brasil. Biol., 50(1):218; H 9 , Jamaica, B.W.I. (British West Indies), St. Andrew, Morcesgop, 8 August 1959, T. S. Parr; CAS (ex JCMC).
Clypeocoris amazonicus Carvalho, 1989
Rev. Brasil. Biol., 49(2):444; figs. 1-5; H ô, Maturacá, Estado do Amazonas, Alto Rio Cauboris, Brasil, 28:XII.65-5.I.63, J. Bechyné; MN.
Colimacoris nicaraguensis Carvalho, 1992
Rev. Nica. Ent., 21:30, fig. 1; H $\ddagger$, Nicaragua, 50 km E Matagalpa, El Coyolar, 20.X.91, 800 m, J. M. Maes, S. Hue, X. Palacios col.; P 1\%; MEESA.

Colimacoris salvadorensis Carvalho, 1989
Rev. Brasil. Biol., 49(1):263, figs. 3-6; H ô, El Salvador, La Libertad, Hacienda Argentina, 17.VI.1960, Rec. J. Bechyné; IRSN.
Collaria boliviana Carvalho, 1990
Revta. Brasil. Ent., 34(2):447, figs. 5-8; H 9 , Rurrenabaque, Beni, Bolivia, Dirings; P 3ôó, 4와; MZUSP.
Collaria manoloi Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1101, figs. 1-5 (1989); H ô, Ezeiza, Provincia Buenos Aires (Argentina), II.72; P 19; CC.
Crassicornus nicaraguensis Carvalho, 1991
Rev. Nic. Ent., 15:32, figs. 1-4; H ô, Nicaragua, Zel. (Zelaya), Nueva Guinea, 12.III.1986, J. M. Maes; MEESA.

Crassicornus venezuelanus Carvalho, 1989
Rev. Brasil. Biol., 49(2):471, figs. 14-28; H \&, Venezuela, Aragua, Racho Grande, $1.100 \mathrm{~m}, 20$. VII.76, J. A. Clavijo e Vaspe; P 3ồ̂, 1̊; MEFFY.
Cylapocerus amazonicus Carvalho, 1989
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):82, figs. 5-6; H 万, Amazon River, Gurupá to Santarém, Brazil, September 16-17, 1930, Holt, Blake \& Agnostini; MN.
Cylapocerus rondoniensis Carvalho, 1992
Revta. Brasil. Zool., 74(4):480, fig. 3 (1990); H 9 , Pimenta Bueno Rondonia, Brasil, XI.1960, M. Alvarenga col.; MN.

Cylapocerus tucuruiensis Carvalho, 1989

Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):83, figs. 7-8; H \&, Tucurui, Pará, Brasil, 1979, M. Alvarenga; MN.
Cylapocorella nigra Carvalho, 1989
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):86, figs. 9-12; H ô, Nova Teutonia,
Santa Catarina, Brasil, $27^{\circ} 11^{\prime} \mathrm{N}, 52^{\circ} 23^{\prime}$ W, April 1969, Fritz Plaumann; MN.
Cylapocoris salvadorensis Carvalho, 1989
Rev. Brasil. Biol., 49(1):266, fig. 8; H i, El Salvador, Volcan San Vicente, Fina [sic for Finca] La Paz, 1.VIII.1959, J. Bechyné; IRNC.
Cyclapocorisca nordestina Carvalho, 1989
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(1):87, figs. 15-16; H ô, Caruaru, Pernambuco, Brasil, IV.1972, M. Alvargenga; P 5ô̊̂, 3̊̊\% MN.
Cylapocoroides centraliss Carvalho, 1989
Rev. Brasil. Biol., 49(2):446, figs. 6-9; H ô, Rio de Janeiro, Floresta da Tijuca, Brasil, GB (Estado da Guanabara, atual Estado do Rio de Janeiro; P 2 ôô; MN. Cyrtocapsus bolivianus Carvalho, 1990

Revta. Brasil. Ent., 34(2):450, fig. 9; H 9, Puenta Villa, Yungas, Bolivia, Dirings;
P 11\%; MZUSP.
Cyrtotylus antoninensis Carvalho, 1989
Rev. Brasil. Biol., 49(2):446, figs. 10-11; H \&, Antonia, PR (Estado do Paraná,
Reserva Sapitanduva, Brasil, 03.XI.1986, Levi. Ent. Profaupar; MN.
Cyrtotylus catarinensis Carvalho, 1989
Rev. Brasil. Biol., 49(2):448, figs. 12-16; H ô, Brasilien, Nova Teutónia, Santa Clara, $27^{\circ} 11^{\prime} \mathrm{W} 52^{\circ} 23^{\prime} \mathrm{L}$, Fritz Plaumann, 300-500 m, 14.XII, 1949; P 1ô, 1 ̣; MN. Cyrtotylus cruciatus Carvalho \& Carpintero, 1991

An. Acad. Brasil. Ci., 63(1):34, fig. 2; H $\ddagger$, San Marcos Sierra, Cordoba, Argentina, II.89, D. J. Carpintero; P 1\%; CC.

Cyrtotylus ruber Carvalho \& Carpintero, 1991
Rev. Brasil. Biol., 51(4):769, figs. 15-19; H ô, Oran, Salta (Argentina), III-69, Diego L. Carpintero; CC.

Cyrtotylus venezuelanus Carvalho, 1989
Rev. Brasil. Biol., 49(2):471, fig. 29; H \&, Venezuela, Bolivar, El Dorado, Santa Elena, km 121, 1.000 m, 26.X.72, J. e L. Bechyné leg.; MEFFY.
Deraeocapsus panamensis Carvalho, 1992
Revta. Brasil. Zool., 7(4):477, fig. 1 (1991); H \&, Panama, CZ (Canal Zone), at light, Fortuna, V.77, Hank Wolda; NMNH.
Derophthalma rizzoi Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):335, figs. 1-5; H 9 , Ca. del Obispo, Salta, Argentina, $2.600 \mathrm{~m}, \mathrm{I} .86$, Carpintero; P 1ô, 6\%\%; CC.
Dijocaria morali Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):35, figs. 3, 13-16; H \& , San Marcos Sierra, Cordoba, Argentina, II.89, D. J. Carpintero; P 1ô, 1̊; CC.
Dijocaria oculata Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):36, figs. 4, 17-19; H ô, San Marcos Sierra, Cordoba, Argentina, I.90, D. J. Carpintero; P 20ô̂̉, 2̊\%; CC.
Dijocaria pulcherrima Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):37, figs. 5, 20-22; H ô; San Marcos Sierra, Cordoba, Argentina, II.89, D. J. Carpintero; P 5ô̧̂̂, 7ịq; CC.

Dijocaria sanmarcosiana Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):39, figs. 6, 23-25; H ô, San Marcos Sierra, Cordoba, Argentina, II.89, D. J. Carpintero; P 28ôô, 16̊̊; CC.
Diplozona brasiliana Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(1):176, figs. 1-5, 32-33; H ठ̂, Diamantino, Fazenda Sao Joao,
MT (Mato Grosso), Brasil, Km 20, BR 163, Roppa; P 6ôô, 7 9 ºf MN.
Diplozona equatoriana Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(1):180, figs. 14-18, 32-33; H ô, Estirao do Equador, AM (Amazonas), Brasil. X.79, M. Alvarenga; P 1\%; MN.
Diplozona quadalupensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(1):182, figs. 19-23, 32-33; H ô, Guadeloupe; NMNH.
Divisotylus costai Carvalho, 1990
An. Acad. Brasil. Ci., 62(4):409, figs. 1-4; H ô, Encruzilhada, Bahia, Brasil, Seabra e Roppa col.; MN.
Dolichomiris planifrons Eyles \& Carvalho, 1975
J. Nat. Hist., 9:262, figs. 15-19; H ô, Republic of South Africa: Rustenburg, 4-xii.1951, A. L. Capener; P 1ô, 1я; NMNH.
Dolichomiris uniformis Eyles \& Carvalho, 1975
J. Nat. Hist., 9:265, figs. 31-36; H ठ̂, India, Pulney Hills, Kodaicanal, 6,500 ft, xi.1953, P. S. Nathan; P 1ố; NMNH.

Eccritotarsus anolaimus Carvalho \& Costa, 1989
Revta. Brasil. Ent., 33(1):67, figs. 3, 5-7; H đ̂, Anolaima, Cundinamarca, Colombia, 8.VI.48, altitude $1.895 \mathrm{~m}, \mathrm{~B}$. Chara; P 2ઠ̊ઠ̧; MEFLG.

Eccritotarsus boconensi Carvalho, 1989
Rev. Brasil. Biol., 49(2):473, figs. 30-33; H ô, Venezuela, Merida, Carbonera, 2.600 m, 8.X.69, J. e L. Bechyné leg; P 3ôơ; MEFFY.
Eccritotarsus cascaensis Carvalho \& Costa, 1989
Revta. Brasil. Ent., 33(1):68, fig. 1; H \& , Cascas, Peru, 1.200 m, Weyrauch; NMNH.
Eccritotarsus chorrensis Carvalho \& Costa, 1989
Revta. Brasil. Ent., 33(1):70, figs. 4, 8-1 1; H ठ̂, Los Chorros, El Salvador, VI.20.1963, D. Q. Cavagnaro e M. E. Irwin; CAS.

Eccritotarsus maesi Carvalho, 1991
Rev. Nica. Ent., 15:34, figs. 5-9; H ô, Nicaragua, Jinotega, 5 km E., VII.89, F. Reiboldt; P 19; MEESA.
Eccritotarsus meridanus Carvalho, 1989
Rev. Brasil. Biol., 49(2):473, figs. 34-39; H ô, Venezuela, Merida, Carbonera, 2.600 m, 8.X.69, J. \& L. Bechyné; P 3ồó; MEFFY.
Eccritotarsus micheli Carvalho, 1992
Rev. Nic. Ent., 21:36, figs. 2-5; H ô, Nicaragua, 50 km E Matagalpa, El Coylar, 20.X.91, J.M. Maes, S. Hue, X, Palacios; MEESA.

Eccritotarsus palmirensis Carvalho \& Costa, 1989
Revta. Brasil. Ent., 33(1):71, figs. 2, 12-15; H, Palmira (Colombia), Vale del Cauca, agosto 1944, B. Losada S; MEFLG.
Eccritotarsus pycnoderoides Carvalho, 1989
Rev. Brasil. Biol., 49(1):265, fig. 7; H 9, El Salvador, El Boqueron, 10.VI.1959, Réc. J. Bechyné; IRNC.
Eccritotarsus villetanus Carvalho \& Costa, 1989

Revta. Brasil. Ent., 33(1):72, figs. 16-20; H of, Villeta, Cundinamarca, Colombia, 13:VI.1965, J. R. Ramos col.; P 1ô, MEFLG.
Eubatas lombardensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(4):415, figs. 1, 9-14; H $\delta$, Sierra Lombard, Limao, 10.8.61, Brasil, Amapá, J. \& L. Bechyné; P 28ơơ, 32̣̊̊; MN.
Euchilocoris corcovadensis Carvalho, 1990
An. Acad. Brasil. Ci., 62(1):70, figs. 1, 9-11; H ô, Corcovado, Rio de Janeiro, Brasil, XII.89, P. Magno; P 1\%; MN.
Eurychilella amazonica Carvalho, 1989
An. Acad. Brasil. Ci., 61(1)105, fig. 1; H \&, Amazonas, Brasil, Eirunepé, VI. 50, J. C. M. Carvalho col.; MN.

Eurychilella callangana Carvalho, 1990
Rev. Brasil. Biol., 50(3):767; new name for preoccupied Eurychilella peruana Carvalho, 1989, see below.
Eurychilella caruaruensis Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):105, fig. 2; H \&, Caruaru, Pernambuco, Brasil, IV.72, M. Alvarenga col.; MN.

Eurychilella paraensis Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):106, fig. 3; H \&, Marituba, 10.VI.1961, Brasil, PA (Pará), J. \& B. Bechyné; MN.
Eurychilella peruana Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):107, figs. 4-10; H \& C Callanga, Peru; P 1ô; NMNH [preoccupied, see Eurychilella callangana].
Eurychilella venezuelana Carvalho, 1989
An. Acad. Brasil. Ci., 61(1): 109, figs. 11-16; H ơ, Venezuela, Aragua, El Limón, July 4, 1968, J. Maldonado C.; NMNH.
Eustictus argentinus Carvalho, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(2):215, figs. 6-9; H ठ̂, Argentina, Meloidie, Misiones, H. L. Parker; MLP.
Eustictus californicus Carvalho \& Costa, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 6(2):182, figs. 1-4; H ó, Mex. (Mexico), Baja California, Su, 14 m E of Guerrero Negro, 11.VIII,71, H. G. Real \& R. E. Main; P 2ơ̂ô 1q; NMNH.
Eustictus itatiaiensis Carvalho, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(2):218, fig. 10; H \&, Parque Nacional do Itatiaia, Rio de Janeiro, M. Alvarenga; MN.
Eustictus membagilus Carvalho \& Costa, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 6(2):184, figs. 5-9; H ô, Nicarágua, V. Membagil, XI.89, J. C. Canter; MEESA.
Eustictus nicaraguensis Carvalho \& Costa, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 6(2):185, figs. 10-13; H of, Nicarágua, Leon,

Eustictus panamensis Carvalho, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(2):219, figs. 11-14; H \& Las Cumbres, Panama, $9^{\circ} 6^{\prime} \mathrm{N}, 79^{\circ} 32^{\prime} \mathrm{W}$, Light trap, 14.iv-74, Hank Wolda; NMNH.
Eustictus sonorensis Carvalho \& Costa, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 6(2):187, figs. 14-18; H 9 , Mex. (Mexico), Sonora, Alamos, 12.VIII.60, P. H. Arnaud Jr., E. S. Ross, D. C. Rentz; P 1ơ; CAS.

Eustictus venezuelanus Carvalho, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(2):221, figs. 15-18; H đ̂, Venezuela, Guar, 12 km S Calabozo, 6-12.II,1969, P. \& P. Spangler; P 1\%; NMNH.
Falconia jamaicensis Carvalho, 1990
Rev. Brasil. Biol., 50(1):198, fig. 13; H \&, Mandeville, Jamaica, Jan. Apr. 1906, Van Duzee; P 1ồ 1 t; CAS.
Falconia veneciana Carvalho, 1990
An. Acad. Brasil. Ci., 62(2): 171, figs. 3, 20-23; H ô, Venecia, Antioquia, Colombia. Octubre 1985, A. Madrigal; P 2ờ̛̀; MEFLG.
Fulviella australiana Carvalho, 1991
An. Acad. Brasil. Ci., 63(4):405, figs. 1-6; H ô, Hogan R., New South Wales, J. Armstrong; ANIC.
Fulvioaustrus montheiti [sic, for monteithi] Carvalho, 1991
An. Acad. Brasil. Ci., 63(4):404, figs. 14-1 5: H \%, Upper Finch Hatton, CK, via Finche Hatton, N. Queensland, 3.1.1961, G. Montheiti [sic]; ANIC.
Ganocapsisca joanensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):200, figs. 1, 9-11; H ô, Fazenda Sao Joao, Diamantino, MT (Mato Grosso), Brazil, 400 m, II.1981, M. Alvarenga; P 19; MN.
Garganisca itatiaiensis Carvalho, 1990
An. Acad. Brasil. Ci., 62(1):76. figs. 1-4; H \&, Brasil, RJ, Itatiaia, Janeiro 1978, Carvalho \& Schaffner; P 19; MN.
Garganus andinus Carvalho, 1992
Revta. Brasil. Ent., 36(3):647, figs. 1-4; H ठ̂, Peru, Satipo, 16.VII. 1985, Arellano

Garganus argentinus Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):336, fig. 6; H \&, Vale de Chanchamayo, Peru, 800 m , VIII-51; P 1ô, 2о̊; CC.
Garganus venezuelanus Carvalho, 1992
Revta. Brasil. Ent., 36(3):649, figs. 5-8; H ठ̂, El Valle, Venezuela, D.F., 10.II.950, F. Fernandez; P 4ôô, 3ịq; MEFFY.

Garganus vilcanensis Carvalho, 1992
Revta Brasil. Ent., 36(3):649, figs. 9-12; H \&, Peru, Amazonas, El Molino (UA, 594.89) Melendez col.; P, 6o̊̊, 7̊̊̊; NMNH.

Gaveanus amapaensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):200, figs. 2, 12-14; H \& , Rio Casaiporé (Brasil), AP (Amapá); J \& B. Bechyné col.; P 19; MN.
Goiastylus goianus Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):45, fig. 2; H 9 , (Brasil), Jatahy (Jataí), Provincia de Goyaz (Estado de Goiás), Bresil; MN.
Guanabarea bicolorides Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 50(3):788, figs. 10-13; H 9 , Sumalao, Salta, Argentina, I.86, Carpintero col; CC.
Guanabarea fasciata Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 50(3):787, figs. 14-17; H ô, Chicoana, Salta, Argentina, 1.600 m, I.86, Diego L. Carpintero; CC.
Guanabarea mariana Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 50(3):787, figs. 18-20; H \&, Santa Maria, Misiones, Argentina, XII.46, Viana col.; CC.

Guapimirella pauloi Carvalho, 1990
Bol. Mus. Para. E. Goeldi, ser. Zool., 5(2):214, figs. 1-5; H ठ̂, Brasil, Rio de Janeiro, Guapimirim, XII.87, P. R. Magno; P 1\&; MN.
Guianella paraibensis Carvalho \& Costa, 1992
An. Acad. Brasil. Ci., 64(2): 194, figs. 1, 10-12; H ô, Juazeirinho, Soledade, Paraiba, Brasil, 16.III.1956, A. G. R. Silva; MN.
Hadronemella jiparaensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):202, figs. 3, 15-17; H ô, Brasil, Rondônia, Ji-Paraná, 7.II.1983, Gleba "G", equipe J. R. Arias; MN.

Hadronemella patagonica Carvalho \& Carpintero, 1991
Rev. Brasil. Biol. 51(4):770, figs. 20-24; H ô, Neuquén, Argentina; P 1ố, 4\%̊; CC.
Hadronemella piraporensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):202, figs. 4, 18-20; H ô, Brasil, Ninas Garias, Pirapora, XI.1976, Seabra, Roppa, Monné col.; MN.

Hadronemella rionegrensis Carvalho \& Carpintero, 1991
Rev. Brasil. Biol., 51 (4):771, figs. 25-28; H ô, Cnel. Gomes, Rio Negro, XI-45; CC.
Hadronemella sanluisensis Carvalho \& Carpintero, 1991
Rev. Brasil. Biol., 51(4):771, figs. 29-33; H ô, S. Gerónimo, San Luis, Arg., I-72, Viana; P 6ôô, 3̊̊; CC.
Hadronemella vermelhensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):205, figs. 5, 21-23; H \& , Aguas Vermelhas, MG (Minas Gerais), Brasil, XII.83, M. Alvarenga; P 1̊́, 1\&; MN.
Herdonoides paulistanus Carvalho, 1989
Rev. Brasil. Biol., 49(2):45 1, figs. 17-22; H ô, Sao Paulo, Brasil, Campos do Jordao, 23.XII.1944, F. Lane col.; MZUSP.

Horcias (Horciasoides) chapadensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(4):417, figs. 2, 12-14; H ô, Chapada dos Guimaraes, 22.I. 961 , Brasil, Mato Grosso, J. \& B. Bechyné; P 1ô, 1 ; MN.

Horcias (Horciasoides) juinensis Carvalho \& Costa, 1991
An. Acad. Brasil, Ci., 63(4):417, figs. 3, 15-17; H đo, Juina, Mato Grosso, V.1985, Roppa; P 3ổ̊; MN.
Horcias (Horciasoides) oestensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(4):419, figs. 4, 18-20; H ô, Ouro Preto, Rondonia, Brasil, VIII.66, Roppa; MN.

Horciasinus neotropicalis Carvalho \& Carpintero, 1992
An. Acad. Brasil. Ci., 64(1):94; H ô, Chavantina, N. (Mato) Grosso, VII.62, Alvarenga col.; P 150 ô, $22 \% \%$; NM. This name proposed for the species which Carvalho and Jurberg (1976) misidentified as Horciasinus tucumanus (Berg). See Rev. Brasil. Biol., 36(4):828, figs. 36-40, 56, 64, for description and illustrations.
Horciasoides ouropretanus Carvalho, 1989
Rev. Brasil. Biol., 49(2):45 1, figs. 23-26; H ô, Topázios, Ouro Preto, Minas Gerais, Brasil, 22.II.1962, J. Bechyné col.; P 2ôô, 1̊; MZUSP.
Hyaliodes meridanus Carvalho, 1989
Rev. Brasil. Biol., 49(2):474, figs. 40-43; H ô, Venezuela, Merida, Cutata, 21.II.1969, J. \& B. Bechyné; P 1ớ; MEFFY.

Ilnacora sonorensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):107, fig. 104; H 9 , Carretera 15, Son. (Sonora), Mex. (México), VII. 29, 1967; P 1ơ, 1̊; CAS.

Ilnacora tepicensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):107, figs. 5-8; H q; Mex. (México), Nayarit, $24 \mathrm{mi} \mathrm{S}. \mathrm{Tepic}$, VIII.16.60, P. H. Arnaud Jr., E. S. Ross, D. C Rentz; P 1ઠ; CAS.

Itacoris peruanus Carvalho, 1991
Rev. Peru. Ent., 33:33, figs. 2, 12-14; H ठ, Chanchamayo (Peru), 16.VIII.1985. Arellano sp., UA, 1948.85; P 3와; MEUNAM.
Juinacoris hugo Carvalho \& Costa, 1990
Mem. Inst. Oswaldo Cruz, 84(IV):91, figs. 1-5; H đ̂, Juina, MT (Mato Grosso), Brasil, V.85, Roppa; P 19; MN.
Juinia castaneus Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):71, figs. 11-14; H 今̂, Brazil: Nova Teutonia, Santa Catarina, $27^{\circ} 11^{\prime}$ N $52^{\circ} 23^{\prime}$ W, November 1971, Fritz Plaumann; P 3iq; MN.
Knightonia incachaca Carvalho, 1990
Revta. Brasil. Ent., 34(2):450, figs. 10-15; H if, Cochabamba, Bolivia, VIII.56, 3.100 m, Dirings; P 1ổ̊; MZUSP.

Lampethusa vigntuni Carvalho, 1990
Caatinga, 7:15, figs. 1-4; H t, Brasil. Estrada Rio-Bahia, Motel da Divisa, 96 m, Encruzilhada, Bahia, XI.1972, Seabra \& Roppa; P 21ô̊̂, 27ǫ̣; MN.
Lapazphylus lapazensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):109, figs. 9-13; H ơ; 10 mi NW La Paz, L. (Lower) Califórnia, X.6.41, Ross \& Bohart, P 2ôờ; CAS.
Leonia fracta Carvalho, 1991
Rev. Nica. Ent., 15:38, fig. 10; H 9 , Nicaragua, Leon. MEESA.
Lestonisca tafoensis Carvalho, 1989
An. Acad. Brasil. Ci., 60(3):330, figs. 1-7 (1988); H ô, Tafo, Ghana, 14.I.66, D. Leston col.; P 2ઠ̊ઠ̧; BMNH.
Liliancoris nigrus Carvalho, 1989
Rev. Brasil. Biol., 49(2):454, figs. 27-31; H ㅇ, Mar de Espanha, Minas Gerais, Brasil, 27-28.II.1962, J. Bechyné col.; P 2ઠิઠิ, 3꽈; MZUSP.
Lundiella rubrocunealis Carvalho, 1990
Rev. Brasil. Biol., 50(2):501, figs. 11-14; H ồ, Colombia, Mosquera Cund. (Cundinamarca), Oak Forest, 22 May 1965, J. A. Ramos; NMNH.
Lundiella tingomariana Carvalho, 1990
Rev. Brasil. Biol., 50(2):502, fig. 15; H 9 , Peru, 50 mi S Tingo Maria, Carpish Crest, XII.28.1954, E. I. Schlinger e E. S. Ross; CAS.
Lygocoris taprobanensis Carvalho, 1992
Rev. Brasil. Biol., 52(1):57, figs. 1-4; H đ̂, Ceylon, N. E. District, Kanda-ela Reservoir, 5.6 mi SW Nuwara Eliya, 6,200 ft, 10-21 Feb. 1970, Davis \& Rowe; P

Mecistosceloides tonkinensis Carvalho, 1992
Revta. Brasil. Ent., 36(4):853, fig. 2; H ô, Vietnam, Tonkin, Chapa, June, 1916, R.V. de Galvaza; BMNH.

Melanotrichus calderensis Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(1):40, figs. 7, 26-28; H 9 , R.9, Km 1,650, Do La Caldera, Salta, Argentina, 1.300 m, I.86, Carpintero; P 1ơ; CC.
Melanotrichus clarensis Carvalho, 1990
An. Acad. Brasil. Ci., 62(4):395, figs. 2, 9-11; H ô, Aguas Claras, MG (Minas Gerais), Brazil, XII.83, M. Alvarenga col.; MN.

Melanotrichus joacemensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):205, fig. 6; H 9 , Joacema, Senhor do Bonfim, Bahia, Brazil, Caatinga, J. C. M. Carvalho; P 19; MN.
Melanotrichus membranosus Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):205, figs. 7, 24-26; H ó, Aguas Vermelhas, MG (Minas Gerais), Brasil, XII.83, M. Alvarenga col.; MN.
Melanotrichus sumalaoensis Carvalho \& Carpintero, 1991
Rev. Brasil. Biol., 51(4):773, figs. 34-37; H ô, Sumalao, Salta, Arg., I-86, Carpintero; P 1ó, 19; CC.
Melanotrichus vermelhensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(2):207, fig. 8; H \& Aguas Vermelhas, MG (Minas Gerais), Brasil, XII.83, M. Alvarenga col.; MN.
Mendozaphylus mendocinus Carvalho \& Carpintero, 1991
An. Acad. Brasil. Ci., 63(2):201, figs. 1-6; H ô, Argentina, Mendoza, Nacunan, XI.77; P 6ơó; CC.

Microoculis nuwarensis Carvalho, 1992
Rev. Brasil. Biol., 52(1):59, figs. 5-7; H of, Sri-lanka, N.E. District, Nuwara Elyia, black light trip (sic, for trap), 2-4. IX. 1975, D. M. Davis, S. Karunarancte (sic, for Karunaratne), D. W. Balooseiya; NMNH.
Microoculis srilankensis Carvalho, 1992
Rev. Brasil. Biol., 52(1):60, figs. 8-11; H ô, Sri-lanka, N. E. District, Mt. Pidurutalagala, 6.500-6.700 ft, 8 October 1976, col. G. F. Hevel, R. E. Dietz, N. S. Karunaratacne (sic, for Karunaratne), J. W. Balasoriya; NMNH.
Mimoncopeltus cajamarcanus Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):116, figs. 18-21; H ó, Cajamarca, Peru, III.42, 2.700 m, Carpintero; CC.
Mimoncopeltus nigrus Carvalho, 1989
Rev. Brasil. Biol., 49(2):437, figs. 5-6; H ô, Peru, Huanuco Prov., Tingo Maria, June 24, 1982, D.S. Bogar; NMNH.
Mollendocoris peruanus Carvalho, 1992
Revta. Brasil. Ent., 36(3):582, fig. 1; H \&, Peru, Mollendo, Loma Zone, 19.XI.1950, Michelbacher \& Ross; CAS.
Monalocoris nigrocollaris Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):110, figs. 17-20; H ô, Guadeloupe; P 1̊̂, 1̊; NMNH.
Monalocorisca bocaina Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):94, figs. 1-4; H đ̂, Serra da Bocaina, S. J. Barreiro, SP (Sao Paulo), Brazil, I.1969, M. Alvarenga col.; P 3\%\%; MN.
Monalocorisca nordestina Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):95, figs. 5-9; H of, Fazenda Caruaru, Caruaru, Pernambuco, Brasil, M. Alvarenga; P 24ôô, 18if; MN.
Monalocorisca tucumana Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):97, figs. 10-14; H ô, Tucumán, R.A. (República Argentina), $1.000 \mathrm{~m}, \mathrm{X} .1957$, Wygodzinsky col.; P 3if; MLP.
Nanniresthenia golbachi Carvalho \& Carpintero, 1992
Revta. Brasil. Zool., 7(1-2):181, fig. 2; H \&, Catamarca (Argentina), Rodeo, 28:
I.58, R. Golbach; P 2\%я; MLP.

Nanniresthenia heteromorpha Carvalho \& Carpintero, 1990

Rev. Brasil. Biol., 49(4):1116, figs. 22-26; H đ̂, Capilitas, Catamarca, Argentina, 3.000 m, I.86, Carpintero; P 2屯ิઠ; CC.

Nanniresthenia minor Carvalho \& Carpintero, 1992
Revta. Brasil. Zool., 7(1-2):182, figs. 1-3; H ô, Glew, Provincia de Buenos Aires (Argentina), II.78, Carpintero; P 1ठ, 2\%\%; CC.
Nanniresthenia rodeana Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):117, fig. 27; H \&, El Rodeo, Catamarca, Argentina, I.58, Golbach; CC.
Neofurius bolivianus Carvalho, 1990
An. Acad. Brasil. Ci., 62(2):173; H $\delta$, Bolivia, Cochabamba, Germain Col.; NMNH. Neofurius minensis Carvalho, 1989

An. Acad. Brasil. Ci., 61(1):112, figs. 21-24; H $\delta$, Aguas Claras, MG (Minas Gerais), Brasil, XII.83, M. Alvarenga; P 1ठं; MN.
Neophylus sonorensis Carvalho \& Costa, 1992
Rev, Brasil Biol., 52(1)110, figs. 14-18; H ठ̂, Mex. (México), Sonora. 40 mi . N of
Hermosillo, VIII.6.60, P. H. Arnaud, Jr., E. S. Ross e D. C. Rentz; P 5ôô, 1 \& CAS.
Neostenotus elongatus Carvalho, 1990
An. Acad. Brasil. Ci., 62(1):70, figs. 3, 12-15; H of, Aguas Claras, MG (Minas Gerais), Brasil, XII.83, Alvarenga; P 1ઠ̂; MN.
Neostenotus venezuelanus Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):71, figs. 15-17; H 9 , Venezuela, Tachira, Pueblo Hondo, 28 July, 1983, Clark \& Clark; P ô; NMNH.
Nicaraguacoris punctatus Carvalho, 1992
Rev. Nica. Ent., 21:38, fig. 6; H \&, Nicaragua, Managua, 8.xi.91. Col. C. Pineda; MEESA.
Notholopus amapaensis Carvalho, 1991
Bol. Mus. Para. E. Goeldi, ser. Zool., 7(2):178, fig. 1; H \& S Serra do Navio, Brasil, AP (Amapá), 18.6.1961, J. \& B. Bechyné; MN.
Notholopus cacerensis Carvalho, 1991
Bol. Mus. Para. E. Goeldi, ser. Zool., 7(2):179, fig. 2; H \& Porto Esperidiao, Caceres, M. (Mato Grosso), Brasil, XI. 84, Magno \& Alvarenga leg; MN.

Notholopus goianus Carvalho, 1991
Bol. Mus. Para. E. Goeldi, ser. Zool., 7(2):179, figs. 3-6; H \&, Goiaz, Campinas.
Spitz col., Jan. 1936; P 1ô; MN.
Opisthocoris carmelitanus Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(2):206, figs. 1-3; H 9 , Brasil: Minas Gerais, Camo do Rio Claro, janeiro 1978, Carvalho \& Schaffner; MN.
Orthotylus apodiensis Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):305, figs. 1, 9-1 1; H ô, Barbalha, Ceará, Brasil, V.1969, M. Alvarenga; P 1 $\mathbf{\delta}$; MN.

Orthotylus aragarssanus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):307, figs. 2, 12-14; H ô, Aragarças, Goiás, Brasil, Carvalho col.; P 3ôô, 2i̊?; MN.
Orthotylus carioca Carvalho, 1990
An. Acad. Brasil. Ci., 62(4):395, figs. 3, 12-14; H ó, Corcovado, Rio de Janeiro, Brasil, Seabra col., 27.X.74; MN.

Orthotylus castaneus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):307, figs. 3, 15-17; H ठ̂, Faz. (Fazenda) Sao Joao, Mato
Grosso, (Brasil), 400 m, II.1981, M. Alvarengo; MN.
Orthotylus clarensis Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):310, figs. 4, 18-21; H ô, Aguas Claras, MG (Minas Gerais), Brasil, XII.1983, M. Alvarenga; P 2ồó; MN.
Orthotylus paraguaiensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):45, figs. 3, 17-19; H ơ, Paraguay, Horqueta, 1938, Albert Schulz col.; P 1ố; NMNH.
Orthotylus sanguineus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):310, fig. 5; H \&, Estr. (Estrada), Rio-Bahia, Km 965, Motel Divisa, 960 m. Encruzilhada, Bahia, Brasil, XI.72, Seabra \& Roppa; MN. Orthotylus singularis Carvalho \& Carpintero, 1991

Rev. Brasil. Biol., 51(4):776, figs. 38-41; H \&, Iguazu, Misiones, Arg., XII-79, Carpintero; P 2ôઠ, 2\%̊; CC.
Orthotylus sinopensis Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):310, figs. 6, 22-24; H đ, Sinop, $12^{\circ} 31^{\prime} \mathrm{S} 55^{\circ} 37^{\prime} \mathrm{W}$, Km 500-600, Mato Grosso, Brasil, 350 m , Roppa e Alvarenga col.; MN.
Orthotylus teutonianus Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):74, figs. 19-23; H ơ, Brasilien, Nova Teutonia, $27^{\circ} 11^{\prime} \mathrm{S}$ $52^{\circ} 23^{\prime}$ L, 9.1944, Fritz Plaumann; P 1ठ̂; MN.
Orthotylus tijucanus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):312, figs. 7, 25-28; H ô, Tijuca, RJ (Rio de Janeiro,

Orthotylus veraensis Carvalho, 1990
An. Acad. Brasil. Ci., 62(4):397, figs. 4, 15-17; H ð́, Vera, Mato Grosso, Brasil, Alvarenga e Roppa col.; P 1ઠ; MN.
Orthotylus vianai Carvalho \& Carpintero, 1991
Rev. Brasil. Biol., 51(4):776, figs. 42-45; H ठ̂, San Geronimo, San Luis, Arg., I-72, Viana; P 8ổ, 8 호 CC.
Orthotylus xavantinus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):312, figs. 8, 29-31; H \&, Brasil, Mato Grosso, 12³9'S $51^{\circ} 45^{\prime}$ W, 12.XI.1968, W. J. Knight, Gallery Forest, U. V. Light trap, Royal Soc.Royal Geog. Soc., Xavantina-Cachimbo Expediction, 1967-1969, BM 1970-192; P 2ôơ; MN.
Pachypoda chimnorazensis Carvalho, 1990
An. Acad. Brasil. Ci., 62(2):173, figs. 4, 24-28; H ठ, Equador, Chimborazo, Naranjapata, Chilcay, 16.VI.1955, R. Levi Castillo; NMNH.
Pachypoda costaricensis Carvalho, 1990
An. Acad. Brasil. Ci., 62(2):173, fig. 5; H \&, Costa Rica, intercep. at Honolulu, T. H., X.7.53, S. Namibi; NMNH.

Pamillia nicaraguensis Carvalho, 1992
Rev. Nica. Ent., 21:40, figs. 7-10; H đ̂, Nicaragua, Masaya, Las Flores, U. V. light, 5.X.91, J. M. Maes; P 19; MEESA.

Papaveronia bergi Carvalho \& Carpintero, 1992
An. Acad. Brasil. Ci., 64(1):89; H ô, Misiones, Arg. (Argentina), Dep. (Departamento) Concep. (Concepcion), Sta. (Santa) Maria, M. J. Viana, 47755, Almir del., 19.6.61; P 5ơ̂, 1̊; MLP.

Paracoris nordicus Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):46, fig. 4; H $\ddagger$, Brésil du Nord (Estado do Pará). Itaituba, Ost. BH.; MN.
Parafurius amapaaensis Carvalho, 1989
An. Acad. Brasil. Ci., 61(1):112, fig. 25; H \& , Brasil, Amapá. Rio Caxnot, 4.VIII.61, J. \& B. Bechyné; MN.

Parantias columbiensis Carvalho, 1990
Rev. Brasil. Biol., 50(2):503, figs. 16-19; H \& , Colombia, Putumayo, Pepino, Miridor, 1.800 m , Nov. 58, Restrepo col.; NMNH.
Parapycnoderes membranalis Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(1):96, figs. 1, 2-4; H ô, Nicaragua, 5 km E Jinotega, VII.89, F. Reinboldt; P 2ồ́; MEESA.

Parapycnoderes mexicanus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(1):98, figs. 5-8; H ô, Mexico, Oaxaca, $20 \mathrm{~m} \mathrm{~N} \mathrm{Putla}$, August 3, 1978, Feifer, Gruetsmacher, R. \& M. Murray, Schaffner; P 7ôô, 10와; NMNH.
Parapycnoderes nigrifemur Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(1):98; H ठ , Caretillo, Guatemala, C. C. Champion, Distant collection 1911-383; P 39\%; BMNH.
Parapycnoderes pueblensis Carvalho \& Costa, 1990 An. Acad. Brasil. Ci., 62(1):101, figs. 13-15; H ઠ̂, Mexico, Puebla, 4.7 km SW La Cumbre, 5,200 ft, July 23, 1989, Kovarik \& Schaffner; P 1ठ̂; NMNH.
Parapycnoderes veracruzensis Carvalho \& Costa, 1990 An. Acad. Brasil. Ci., 62(1): 101, figs. 16-18; H \$, Mexico, Veracruz, 8 km N Fortin, April 10, 1978, J. C. Schaffner; P 1ô, 1\%; NMNH.
Peltidocylapus tapirapensis Carvalho, 1992
Revta. Brasil. Biol., 74(4):483, fig. 4 (1990); H \&, Brasil, Barra do Tapirapé, MT (Mato Grosso), XI.1964, Boris Malkin; MN.
Pericosia sinaloensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):112, figs. 19-20; H ô, Mex. (México), Sinaloa, 26 mi N Pericos, VIII.13.60, P. H. Arnaud, Jr., E. S. Ross, D. C. Rentz; P 5ô, 1̊; CAS.
Perissobasis hugoi Carvalho \& Costa, 1990
Mem. Inst. Oswaldo Cruz, 84(IV):94, figs. 6-10; H ठ̂, Juina, MT (Mato Grosso), Brasil, V.85, Roppa; MN.
Perissobasis panamensis Carvalho, 1990
Rev. Brasil. Biol., 50(2):503, figs. 20-23; H ô, Panama, Canal Zone, Mojinga Swamp, I.XI.74. Dr. M. Boreham; NMNH.
Perissobasis peruanus Carvalho, 1991
Rev. Peru. Ent., 33:89, figs. 4, 18; H \&, Chanchamayo (Peru), 30.IV.85, Arellano, UA 2079; P 19; MEUNAM.
Perumiris saltensis Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):337, figs. 7-10; H \$ , Chicoana, Salta, Argentina, 1,500 m, I.86, Carpintero; P 3ôô, 2̊̊\% CC.
Phyllofulvius australianus Carvalho, 1991
An. Acad. Brasil. Ci., 63(4):406, figs. 7-13; H ô, Cabbage Tree, CK, Victoria, 8.2.61, N. Dobrotworsky; ANIC.

Phytocoris aconcaguensis Carvalho \& Costa, 1991

An. Acad. Brasil. Ci., 63(1):46, figs. 5, 20-22; H ô, Cachagua, Aconcagua, 5.III.82, (Argentina); P 1ô, 12̊\%; MLP.
Phytocoris alvarengai Carvalho \& Costa, 1991
Rev. Brasil. Biol., 51(2):355, figs. 1-6; H ô, Aguas Claras, MG (Minas Gerais), Brasil, XII.83, Alvarenga col; P 19; MN.
Phytocoris bahiensis Carvalho \& Costa, 1991
Rev. Brasil. Biol., 51(2):357, figs. 7-11; H ô, Estrada Rio Bahia, Km 865, Encruzilhada, Bahia, Brasil, 906 m, XI.1972; MN.
Phytocoris boyacanus Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):771, figs. 1-4; H 九̂, Colombia, Guateque, Boyaca, 6 Nov. 1965, J. A. Ramos col; P 6ỡó, 4ị; NMNH.
Phytocoris clarensis Carvalho \& Costa, 1991
Rev. Brasil. Biol., 51(2):358, figs. 12-16; H ô, Aguas Vermelhas, MG (Minas Gerais), Brasil, XII.83, Alvarenga col.; P 3ổ̂, 5̣̊̊; MN.
Phytocoris columbiensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):771, figs. 5-8; H ô, Colômbia, 9 km S of Fusagasuga, Cundinamarca, J. A. Ramos col; P 1ô, 2ई̣; MEFLG.
Phytocoris coquimbensis Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):338, figs. 11-15; H ô, Vicuna, Coquimbo, Chile, X.83, Peña; P 23ơす'; CC.
Phytocoris costaricensis Carvalho, 1990
Rev. Brasil. Biol., 50(3):765, figs. 1-5; H ô, Costa Rica, Cerro La Muerte, 3.100 m, 5-7.VIII.1981, V. O. Becker col.; NMNH.
Phytocoris diamantinensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):755, fig. 1; H 9 , Diamantino, Fazenda Sao Joao, Mato Grosso, Brasil, km 20 Br 163, Roppa col.; MN.
Phytocoris divisensis Carvalho and Costa, 1991
Rev. Brasil. Biol., 51(2):361, figs. 17-21; H ô, Estrada, Rio-Bahia, km 965, Encruzilhada, Bahia, Brasil, 900 m, XI.1972, Seabra e Roppa; P 8ôô, 6̊ㅘ; MN.
Phytocoris ecuadorensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):773; H ठ̂, San Isidro, W. Loja, Ecuador, 14.65, L. F. Peña; P 3 $\hat{\text { ôs }}$. Based in part [emitting Guatemal and Panama records] on treatment of Phytocoris vilis (Distant) by Carvalho and Gomez, 1969, An. Acad. Brasil. Ci., 41(3):424, figs. 12-18; NMNH.
Phytocoris fiuzai Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):756, figs. 2-6; H ô, Viçosa, MG (Minas Gerais), Brasil, 13.X.82, Fiuza e Martins col.; MN.

Phytocoris garagoensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):773, figs. 9-13; H ô, Colômbia, Rio Garagoa, Boyaca, J.
A. Ramos col.; 2ôठ̂, lq; NMNH.

Phytocoris itajaiensis Carvalho \& Costa, 1992
Rev. Brasil. Biol., 52(1):74, figs. 24-27; H ô, Nova Teutonia, Santa Catarina, Brazil,
$27^{\circ} 11^{\prime} \mathrm{N} 52^{\circ} 23^{\prime} \mathrm{W}$, December 1969, Fritz Plaumann; P 2 ôô, 2 ợ; MN.
Phytocoris jacareacanga Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):758, figs. 7-10; H ô, Jacareacanga, Pará, Brasil, XII.1988, M. Alvarenga col.; MN.

Phytocoris juinensis Carvalho \& Costa, 1991

Rev. Brasil. Biol., 51(2):361, figs. 22-25; H ô, Juina, Mato Grosso, Brasil, V.85, Roppa; MN.
Phytocoris matogrossensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):760, figs. 11-15; H ó, Diamantino, Fazenda Sao Joao, MT (Mato Grosso), Brasil, km 29, Br 163, O. Roppa col.; MN.
Phytocoris melendezae Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):775, figs. 14-18; H \&, Colpa, Amazonas, Peru, 15.XII.1984, E. Melendez; MEUNAM.

Phytocoris ouropretanus Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):760, figs. 16-20; H ô, Ouro Preto, Rondônia, Brasil, VII.86, O. Roppa col.; MN.

Phytocoris panamensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):48, figs. 6, 23-25; H đ , Panama, Chiriqui Dist., Renascimiento, Santa Clara, 4,000 ft 28-29. V.76; P 1ठ̂, 2q̊? NMNH.
Phytocoris plaumanni Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(2):301, figs. 2, 8-10; H $\delta$, Nova Teutonia, Santa Catarina, Brasil, $27^{\circ} 11^{\prime} \mathrm{S} 52^{\circ} 27^{\prime} \mathrm{W}$, October, 1969, Fritz Plaumann; P 21ô̊̂, 23̣̊̊; MN.
Phytocoris rondoniensis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):763, figs. 21-26; H of, Ouro Preto, RO (Rondônia), Brasil, VII.86, Roppa col.; MN.

Phytocoris sulinus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(2):303, figs. 4, 11-14; H ô, Nova Teutonia, Santa Catarina, Brasil, $27^{\circ} 11^{\prime}$ S $52^{\circ} 23^{\prime}$ W, December 1969, Fritz Plaumann; P 1ô, 1̊; MN.
Phytocoris teutonianus Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(2):303, figs. 3, 15-18; H ô, Nova Teutonia, Santa Catarina, Brasil, $27^{\circ} 11^{\prime} \mathrm{S} 52^{\circ} 27^{\prime} \mathrm{W}$, December 1969, Fritz Plaumann; P 6ổત, 5\%̊ㅇ MN.
Phytocoris triumphalis Carvalho \& Costa, 1990
Rev. Brasil. Biol., 50(3):777, figs. 23-27; H ô, Colombia, El Triumfo, Cundinamarca, 11 dez. 1965, J. A. Ramos col.; P 2\%9; NMNH.
Phytocoris venezuelanus Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):48, figs. 7, 26-28; H ô, Venezuela, Aragua, Rancho Grande, 20 km N of Maracay, 28 July 1976, 1,100 m, M. H. Sweet, V.46; P 2\%я; NMNH.
Phytocoris veraguasinus Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):51, figs. 8, 29-31; H ô, Panamá, Santa Fé, Veraguas, 2,900 ft. 15 Feb 74, col. D. Engleman; NMNH.
Phytocoris vicuniensis Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):339, figs. 16-19; H ô, S. Vicuña, Coquimbo, Chile, X.83, Peña; P 5ôô, 2 \%̊; CC.

Phytocoris vossoroca Carvalho \& Costa, 1991
Rev. Brasil. Biol., 51(2):364, figs. 26-30; H ô, Vossoroca, PR (Paraná), (Brasil), Tijuca do Sul, Olaf Mielke col., II.79; P 2 ôô, 7 q̊; MN.
Phytocorisca catarinensis Carvalho \& Costa, 1990
An. Acad. Brasil. Ci., 62(3):299, figs. 1, 5-7; H ô, Nova Teutonia, Santa Catarina, Brasil, $27^{\circ} 11^{\prime}$ S $52^{\circ} 27^{\prime}$ W, July 1970, Fritz Plaumann; P 8ô̊, $9 \not 9 \ddagger ;$ MN.
Pilosicerus rondoniensis Carvalho, 1992

Revta. Brasil. Ent., 36(3):583, fig. 2; H \&, Brasil, Rondônia, Ouro Preto, VI.86, Roppa col.; MN.
Platyscytus clorindae Carvalho, 1991
Rev. Peru. Ent., 33:89, figs. 3, 15-17; H ô, Chanchamayo (Peru), 16.VIII.85, Arellano, UA 1647.85; P 1ô, 6ị? MEUNAM.
Platytylus dureti Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4): 1119 , figs. 28-30; H $\delta$, Iquazu, Misiones, Argentina, Duret, XI.45; CC.

Platytylus nigrocollaris Carvalho, 1989
Rev. Brasil. Biol., 49(2):437, figs. 10-10a; H ठ̂, Brasil, Santa Catarina, Nova Teutonia, $27^{\circ} 11^{\prime} \mathrm{S} 53^{\circ} 23^{\prime}$ W, Dez. 1988, Fritz Plaumann; MN.
Platytylus peruanus Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1120, figs. 31-34; Hô, Aucayagu, Peru, 4.II.64, Dourojeani; P 4ôô, 1̊; NMNH.
Platytylus trinotatus Carvalho, 1989
Rev. Brasil. Biol., 49(2):439, figs. 11-14; H ठ̂, Brasil, Santa Catarina, Nova Teutonia, $27^{\circ} 11^{\prime} \mathrm{S} 53^{\circ} 23^{\prime}$ W, Jan. 1974, Fritz Plaumann; P 2ôô; MN.
Pliniella columbiensis Carvalho, 1989
Rev. Brasil. Biol., 49(2):475, figs. 44-48; H ô, Prima, Colombia, Santander del Norte, $1.700 \mathrm{~m}, 27 . V .1865$, J. e B. Bechyné leg; P 1ờ; MEFLG.
Pliniella peruana Carvalho, 1991
Rev. Peru. Ent., 33:89, fig. 7; H ô, Chanchamayo (Peru), 26.VIII.86, Arellano, UA 1360.86; MEUNAM.

Poeas gaveana Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(4):419, fig. 5; H ठ', Corcovado, Guanabara, Brasil, X.76, C. A. Campos Seabra; P 1\%; MN.

Poeas goiana Carvalho, 1989
Rev. Brasil. Biol., 49(2):455, figs. 35-38; H đ̂, Fazenda Cachoeirinha, Jatai, Goiás, Brasil, X.1962, Expediçao do Departmento de Zoologia; P 1ô, 2̊̊; MZUSP.
Poeas metaensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(4):420, fig. 6; H \&, Colombia, 3 mi W Villavicencio, Meta, 920 m, III.4.955, E. I. Schlinger e E. S. Ross; CAS.
Poeas minima Carvalho, 1990
An. Acad. Brasil. Ci., 62(1):70, figs. 4, 16-19; H 9 , Sinop, Rio Teles Pires, MT (Mato Grosso), Brasil, Alvarenga \& Roppa; P 2ઠิઠ, 3와; MN.
Polymerus andinus Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):340, figs. 20-23; H ô, Capillitas, Catamarca, Argentina, 3.000 m, I.86, Carpintero; P 1ô, 19; CC.

Prepops bachmanni Carvalho \& Carpintero, 1990
Rev. Brasil. Biol., 49(4):1123, figs. 35-39; H ô, Calamuchita, Cordoba, Argentina, I.78, Carpintero; P 7ôô, 18̊̊; CC.

Prepops bastensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):52, figs. 9, 32-34; H ô, Vila Bastos, Sto. (Santo) André, S. (Sao) Paulo, Brasil, 13.II.1962, L. Stowbunenko col.; MN.

Prepops cajuruensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):52, figs. 10, 35-37; H ô, Cássia dos Coqueiros, Mun (Município) de Cajuru, SP (Sao Paulo), Br (Brasil), XI.XII.1954-I.1955, M. P. Barreto col.; MN.

Prepops caliensis Carvalho, 1989
Rev. Brasil Biol., 49(2):441, fig. 15; H $\$$, Colombia, Valle, 18 km W Cali, 22 June 1982, Clark \& Cave, P 19; NMNH.
Prepops guanduensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):53, figs. 11, 38-40; H or, Baixo Guandu, S. Sto. (Espirito Santo), Brasil, 9-14.XI.70, C. Elias leg.; MN.
Prepops imperatrizensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):54, figs. 12, 41-44; H ô, Imperatriz, MA (Estado do Maranhao), (Brasil), 18.VII.79; MN.
Prepops mariliensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):54, figs. 13, 45-46; H t̂, Marilia, Est, S. Paulo (Estado de Sao), Brasil, 865, II.37, C. O. T. M. col.; MN.
Prepops plaumann [sic] Carvalho, 1989
An. Acad. Brasil. Ci., 61(4):467, figs. 1-4; H ô, Brasil, Nova Teutônia, Santa Catarina, Fritz Plaumann, out, 1967; P 4 ôô; MN.
Prepops procorrrentinus [sic, for procorrentinus] Carvalho \& Carpintero, 1992
An. Acad. Brasil. Ci., 64(1):90; H đ, San Roque, Corrientes, II.20. Bosq; P 21 ôઠ, 17\%\%; MLP. Proposed as new name for species treated as Prepops correntinus (Berg) by Carvalho and Fontes, 1970:370, figs. 12-16.
Prepops rurrenabaquensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):56, fig. 14; H 9 , Bolivia, Rurrenabaque, Beni, 178 mts , Dirings, 961, X.; MN.
Prepops ubirajarai Carvalho, 1989
Rev. Brasil. Biol., 49(2):455, figs. 39-42; H \&, Ribeirao Preto, Fazenda Iracema, Sao Paulo, Brasil, II.XII.1956, Barreto col.; P 1ô; MZUSP.
Prepopsinus paraensis Carvalho \& Costa, 1991
An. Acad. Brasil. Ci., 63(1):57, figs. 15, 47-49; H đ̊, Brasil, Pará, Serra Norte (Carajás) Pojuca, coleta noturna, 16.XI.1985; MN.
Proba gracilioides Carvalho \& Costa, 1989
An. Acad. Brasil. Ci., 60(3):338, figs. 9-13(1988); H ô, Colombia, 30 km W Bogata, Mosuera, 1.800 m , Mar. 65, J. A. Ramos; MEFLG.
Proba nigra Carvalho \& Carpintero, 1989
An. Acad. Brasil. Ci., 61(3):340, figs. 24-28; H ठ̂, Capillitas, Catamarca, Argentina,

Proba saltensis Carvalho \& Costa, 1989
An. Acad. Brasil. Ci., 60(3):341, figs. 20-23 (1988); H \&, Angustura de Arica, Salta, 19.II.54, Wygodzinsky leg; P 1̂̂, 1\%; MLP.

Pseudoloxops dietzi Carvalho, 1992
Rev. Brasil. Biol., 52(1):61, figs. 12-15; H ô, Sri-lanka, Gal. District, Kannelyia, 200 ft , black light, 15-17 October 1976, C. [sic, for G.] F. Hevel, R. E. Dietz, S.
Karunaratacne [sic for Karunaratne], J. W. Balassoriya; P o; NMNH.
Pseudoloxops habaranensis Carvalho, 1992
Rev. Brasil. Biol., 52(1):62, figs. 16-18; H ot, Sri-lanka, Pol. District, 10 mi E of
Habarana, black light, $650 \mathrm{ft}, 12$ November 1976, G. F. Hevel, R. E. Dietz, S.
Karunaratacne [sic, for Karunaratne], D. W. Balassoriya; NMNH.
Pycnoderes centralis Carvalho, 1990
An. Acad. Brasil. Ci., 62(2):174, figs. 6, 29-31; H ó, Nicaragua, 5 km E Jinotega, VII.89, F. Reinboldt; P 4ổત, 3ọ̊; IBUN.

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Rev. Peru. Ent., 33:89, figs. 6, 19-22; H ô, Chanchamayo (Peru), 9.VII.86. UA 1384.86, Arellano; P 3ơô, 3i̊\%; MEUNAM.

Pycnoderes misionensis Carvalho \& Carpintero, 1990
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(México), VI.21.1933, H. E. Hilton e R. L. Usinver [sic, for Usinger]; P 2ôô, 1̊;
CAS.
Resthenia araguana Carvalho, 1989
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Notocyrtus paraensis Carvalho \& Costa, 1992
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## LIST OF JOURNALS CITED BY ABBREVIATIONS

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Revta. Brasil. Zool. - Revista Sociedad Brasileira de Zoologia

## LIST OF ABBREVIATIONS FOR INSTITUTIONS <br> CONTAINING HOLOTYPES

ANIC-Australian National Insect Collection, Canberra
BMNH - The Natural History Museum (formerly British Museum Natural History), London
CAS-California Academy of Sciences, San Francisco
CC—Diego L. Carpintero, personal collection, Buenos Aires
IBUN-Instituto de Biologia, Faculdade de Ciencias, Universidade Nacional Autonoma de Nicaragua, León
IRSN - Institut Royal des Sciences Naturelles de Belgique, Bruxelles
MEESA - Museo Entomologico, Ecole Superior de Agricultura, Leon, Nicaragua
MEFFY - Museu de Entomologia F. Fernandez Yepez, Maracay
MEFLG-Museo Entomologica Francisco Luiz Gallego, Medellin
MEUNAM - Museu da Entomogia da Universidade Nacional Agraria de la Molina, Lima, Peru
MLP—Museu de La Plata, La Plata, Argentina
MN-Museu Nacional de Historia Nacional, Rio de Janeiro
MZUSP - Museu de Zoologia da Universidade de Sao Paulo, Sao Paulo
NMNH - National Museum of Natural History, Washington, D.C.
NZAC—New Zealand Arthropod Collection, Aukland

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## BOOK REVIEW

J. New York Entomol. Soc. 102(4):509-511, 1994

The Bee Genera of North and Central America (Hymenoptera: Apoidea).-Charles D. Michener, Ronald J. McGinley, and Bryan N. Danforth. 1994. Smithsonian Institution Press, Washington, D.C. VIII +209 pp. ISBN 1-56098-256-X cloth. $\$ 45$.

This book is a milestone of great importance in the study of bees. Published exactly 50 years after the appearance of Michener's classic study of bee anatomy, classification, and phylogeny (1944), it will replace the earlier publication as the starting point for serious students who wish to learn the genera of bees and their classification. Michener was the sole author of the first volume, in part his doctoral thesis submitted to the University of California. In the present volume, Michener is joined by McGinley and Danforth, and they are now armed with 50 years of additional knowledge resulting from Michener's own research, that of his numerous students, and that of bee specialists around the world, all of whom were influenced by the original 1944 publication.
The 1944 study was an in-depth investigation into the morphology of bees, followed by sections on their phylogeny and their worldwide classification. Importantly it provided a key to the 93 genera that occurred in America north of Mexico and thus enabled students in North America to become familiar with these taxa. The new volume is in many ways different. Above all else, it focuses on identification of bees to genus. The geographic region covered is the New World from the ColombiaPanama border northward, an area in which 169 genera are recognized. A little more than half of the volume is devoted to taxonomic keys for identification.

The main key to genera is long, consisting of 233 couplets. The authors have cleverly introduced several devices (all actually keys) to decrease the labor in running specimens through the main key. The first device is a set of succinct alternative characterizations (called "locators") of seven groups of genera. If the bee to be identified fits one of these, either the genus can be identified in the short key in the locator or the locator key directs the user to the appropriate couplet in the long key where the specimen can then be run. As another device, a short key to the eight recognized families of bees is presented. Once the family is known (or if it is already known), the user can then turn to the next section "Guide to the Genera of Each Family." This section consists of a short key for each family which leads either directly to a genus in the family or to the section in the main key where the genus can be found. All of the characters used in the keys are illustrated with precise diagrams, SEM micrographs, or photographs which help immensely in conveying often rather complicated anatomical information. These illustrations are found in the keys adjacent to the couplet where they are mentioned, and thus enhance the ease of using the keys.

A noteworthy aspect to this work is that the keys are presented in both English and Spanish, as is the explanation on how to use them. This should significantly help
promote the study of bees in Latin American countries. Other sections of the book are in English alone.

In contrast to the 1944 treatise, discussion of the morphology of bees is limited, but it is entirely adequate for enabling a person unfamiliar with bee anatomy to use the keys. Here again the illustrations are outstanding, well executed and clearly labeled. It is a pleasure to see anatomical terms completely spelled out on diagrams rather than represented by initials that have to be decoded by reference to another section of a work.

The authors tell us that a section of 47 pages entitled "Notes on the Genera" is intended to supplement the key sections to help indicate whether users have been successful in correctly using the keys. It does serve this purpose because it briefly gives the general habitus of each genus which is accompanied in many cases by photographs or drawings. But this section actually accomplishes more: genera are organized by family, subfamily, and tribe. Hence the classification of North and Central American bees is laid out (also done in tabular form in one of the appendices). Here also other information concerning the taxa is mentioned, such as alternative classifications, host-cleptoparasite relationships, and distributions. Of great help is the fact that this section refers the reader to published revisions or other systematic works on the taxa so that specimens can be identified further.

Phylogeny of bees, though of great interest to the authors, is not discussed in the new volume; that subject matter lies beyond the scope of the work.

There are a number of other brief sections to the book. A two-page chapter acquaints the reader with new or unfamiliar nomenclatorial or classificatory changes with respect to North and Central American bees. Appendix A is a checklist of subgeneric, generic, and higher category names of bees arranged in a hierarchy. Appendix B identifies the figure sources. Appendix C, presumably written as a postscript, identifies yet another genus in the area under consideration. Finally, Appendix D advises the reader of some classificatory changes soon to come (already arrived with respect to ongoing studies of long-tongued bees).

The most outstanding strength of this tome is that it is extremely usable and as authoritative as any such treatise can be. It has been thoughtfully planned, superbly executed, and diligently tested by many students and specialists. For persons interested in bees, their classification, behavior, ontogeny, ecology, and impact on agriculture, this book is essential because it is the new "ground zero" for learning about bees. It seems likely that this book will be as influential as Michener's 1944 treatise, which is to say that this new volume should be useful for another 50 years.

When the year 2044 AD arrives, what will the then new "bible" for bees look like and, more importantly, where will our investigations of bees have led us? It seems likely that the answer to the first question is that keys will be largely computerized by that time. The answer to the second question is more nebulous. We can hope works patterned after the "Bee Genera of North and Central America" will have been written for the other continents. We can certainly expect that major advances will have been made in the higher classification by that time and that many taxa will have been revised so that we will have a better understanding of the world's bee fauna at the species level. But of course the study of bees is far more than their systematics. Whatever other advances are made in our understanding of them, there can be little doubt but that the current volume will have played a significant role.-

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| Number 1 |  |
| :---: | :---: |
| Identification of New World Agonum, review of the Mexican fauna, and description of Incagonum, new genus, from South America (Coleoptera: Carabidae: Platynini) James K. Liebherr | 1-55 |
| On the spider genus Meleon Wanless (Araneae: Salticidae) D. P. Wijesinghe | 56-61 |
| Synopsis of the Saicinae (Heteroptera: Reduviidae) of America North of Mexico, with the description of a new species of Saica from the eastern United States <br> R. L. Blinn | 62-66 |
| Oligembia vetusta, a new fossil teratembiid (Embioptera) from Dominican amber Claudia A. Szumik | 67-73 |
| A new species of Aphelocheirus from Sumatra, and addenda to the world checklist (Heteroptera: Naucoridae) <br> Dan A. Polhemus | 74-78 |
| Plusiotis citlaltepetlamayatli, a new species of the lecontei group from Mexico (Coleoptera: Melolonthidae; Rutelinae) <br> Julian Blackaller-Bages and Leonardo Delgado | 79-85 |
| Two new flat bug species from North America (Heteroptera: Aradidae) T. Vásárhelyi | 86-90 |
| Taxonomy and distribution of the Holarctic diving beetle Laccophilus biguttatus Kirby (Coleoptera: Dytiscidae) <br> R. E. Roughley and A. N. Nilsson | 91-101 |
| Aradus pericarti, a new species from South America (Heteroptera, Aradidae) Ernst Heiss | 102-106 |
| The first record of Eremochilini (Coleoptera: Coccinellidae: Epilachninae) from Mexico Robert D. Gordon and Natalia Vandenberg | 107-110 |
| Notes and Comments |  |
| The rediscovery of the Clearwing Chestnut Moth, Synanthedon castaneae (Busck) <br> (Lepidoptera: Sesiidae) in Connecticut <br> Sandra L. Anagnostakis, <br> Kenneth M. Welch, J. Wendell Snow, Kathy Scarborough and Thomas D. Eichlin | 111-112 |
| On the natural history of Canopidae (Heteroptera: Pentatomoidea) Joseph V. McHugh | 112-114 |
| Mycophagous Miridae? Associations of Cylapinae (Heteroptera) with Pyrenomycete Fungi (Euascomycetes: Xylariaceae) <br> Quentin D. Wheeler and A. G. Wheeler, Jr. | 114-117 |

The taxonomic status of Cnemodus inflatus Van Duzee (Hemiptera: Lygaeidae)
James A. Slater and Richard L. Hoffman ..... 117-119
Book Reviews

| Insects of Panama and Mesoamerica: Selected Studies | Morton S. Adams | $120-122$ |
| :--- | ---: | ---: |
| Caterpillars: Ecological and Evolutionary Constraints on Foraging |  |  |
|  | David L. Wagner | $122-124$ |
| The World of Nematodes | Ann E. Hajek | $124-125$ |

## Number 2

Recognition of the West Asian Anchomenus kurnakovi and A. punctibasis (Co-
leoptera: Carabidae: Platynini) and Miocene evolution of the Mediterranean
and Paratethys Seas

James K. Liebherr 127-141 | A new genus and four new species of Colpurini (Hemiptera: Heteroptera: Coreidae) |  |  |
| ---: | ---: | ---: |
| from New Guinea | Harry Brailovsky | $142-153$ |

Hydroptilidae (Trichoptera) of Costa Rica and the Neotropics: Systematics of thegenus Byrsopteryx Flint (Stactobiini)
Steven C. Harris and Ralph W. Holzenthal ..... 154-192
A generic conspectus of the tribe Procleticini Pennington (Heteroptera: Pentatomidae), with the description of Parodmalea rubella new genus and species
D. A. Rider193-221
West Indian Coccinellidae V (Coleoptera): A review of Coccidulini and additions to Psorolyma Sicard Robert D. Gordon ..... 222-231
West Indian Coccinellidae VI (Coleoptera): new genera and species of Sticholo- tidini and a cladistic analysis of included genera Robert D. Gordon ..... 232-241
The stridulatory mechanism of Nerthra Say, a new species, and synonymy (Het- eroptera: Gelastocoridae) John T. Polhemus and Per Lindskog ..... 242-248
A new species of Octotoma Chevrolat, 1837, from Guatemala (Coleoptera: Chrys- omelidae, Hispinae) C. L. Staines ..... 249-250
Pemphigus obesinymphae, a new American aphid species with defenders and swollen nymphs (Homoptera: Aphidoidea: Pemphigidae)
Shigeyuki Aoki and Nancy A. Moran 251-260
A new species of Ambrysus Stål from Ash Meadows, Nevada (Heteroptera: Nau- coridae) John T. Polhemus and Dan A. Polhemus ..... 261-265
Notes and CommentsVibrational signals associated with mating behavior in the treehopper, Enchenopabinotata Say (Hemiptera: Homoptera: Membracidae)Randy E. Hunt266-270
Stridulatory mechanisms in aquatic and semiaquatic Heteroptera
John T. Polhemus ..... 270-274
A replacement name for Myrmecomiris Polhemus and Razafimahatratra (Het- eroptera: Miridae) Dan A. Polhemus ..... 274-275

## Book Reviews

| Beetle Larvae of the World: Interactive Identification and Information Retrieval |
| :--- |
| for Families and Subfamilies |
| Joseph $V$. McHugh |

Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico

Insect Pathology

## Number 3

Absence of kin discrimination behavior in a soldier-producing aphid, Ceratovacuna japonica (Hemiptera: Pemphigidae; Cerataphidini)
Norman F. Carlin, David S. Gladstein, Andrew J. Berry, and Naomi E. Pierce 287-298
Cladistic placement of the Subantarctic genus Haversiella (Coleoptera: Curculionidae) Juan J. Morrone
Fossil Cydnidae (Heteroptera) in the Dominican amber Donald B. Thomas
A new case of parthenogenesis in beetles: Longitarsus melanurus (Melsheimer) (Coleoptera: Chrysomelidae) David G. Furth 310-317
A revision of the genus Thasus (Hemiptera: Coreidae: Coreinae: Nematopodini) Harry Brailovsky, Carl W. Schaefer, Ernesto Barrera and Richard J. Packauskas 318-343
Etapocanga, a new genus and two new species of neotropical flea beetle (Coleoptera: Chrysomelidae: Alticinae)

Catherine N. Duckett
344-349
Description of the larva of an unidentified species of Ceratopus Schoenherr, with comments on plant associations in Ceratopodinae (Coleoptera: Curculionidae)

James Pakaluk and Tami A. Carlow
350-354
A remarkable new bamboo lygaeid from Mexico and a new species of Patritius from Venezuela (Hemiptera: Lygaeidae: Blissinae)

James A. Slater and Harry Brailovsky 355-360
A description of the immature stages of Paduniella nearctica (Trichoptera: Psychomyiidae) with notes on its biology Michael L. Mathis and David E. Bowles 361-366
A new species of Leotichius from Bali, with notes on immature stages and habitat
$\begin{aligned} & \text { (Heteroptera, Leptopodidae) } \\ & \text { John T. Polhemus and Randall T. Schul }\end{aligned}$ 367-373
Two new species of Atractotomus from southern Mexico (Heteroptera: Miridae: Phylinae) Gary M. Stonedahl and Michael D. Schwartz 374-380

## Notes and Comments

Neotype designation for Ranatra americana edentula Montandon (Heteroptera: Nepidae) John T. Polhemus 381-383
Predation by Clivinema coalinga Bliven (Heteroptera: Miridae: Deraeocorinae: Clivinemini) of Orthezia annae Cockerell (Sternorrhyncha: Ortheziidae) Richard S. Miller and Randall T. Schuh 383-384
Megatoma (Pseudohadrotoma) kaliki (Coleoptera: Dermestidae): Range extension and character variation
R. S. Beal, Jr.

384-385
A southern distribution for the introduced dung beetle Aphodius (Otophorus) haemorrhoidalis (L., 1758) Jorge M. Lobo 385-386

## Book Reviews

Behaviour and Social Evolution of Wasps: The Communal Aggregation Hypothesis James M. Carpenter
The Insects of Macau
Richard G. Robbins
389-391

| Proceedings of the Second International Congress of Dipterology Rudolf Meier | 391-394 |
| :---: | :---: |
| Nymphs of North American Stonefly Genera (Plecoptera) Sule Oygur | 394-396 |
| Verzeichnis der Sandlaufkäfer der Welt (Coleoptera, Cicindelidae) |  |
| Sanford Leffler | 396-397 |
| Biology and Conservation of the Monarch Butterfly Andrew V. Z. Brower | 397-399 |
| Butterflies through Binoculars, A Field Guide to Butterflies in the Boston, New York, Washington Region <br> Paul A. Opler | 400-401 |
| A Functional Biology of Parasitism: Ecological and Evolutionary Implications |  |
| Mark E. Siddall | 401-403 |
| Number 4 |  |
| Natural history of leaf-folding caterpillars, Dichomeris spp. (Gelechiidae), on goldenrods and asters | 405-428 |
| A revision of the South American species of the ant genus Probolomyrmex (Hymenoptera: Formicidae) <br> Donat Agosti | 429-434 |
| Larval description of Abaris bigenera Bates, 1882, and notes on relationships of the genus Abaris Dejean, 1831 (Coleoptera: Carabidae: Pterostichini) <br> Yves Bousquet and James K. Liebherr | 435-441 |
| A review of the genus Pseudevoplitus Ruckes (Heteroptera: Pentatomidae), with the description of three new species |  |
| Jocélia Grazia, Miriam Becker, and Donald B. Thomas | 442-455 |
| A new species and new records of Cyclocephala from Guatemala (Coleoptera: Melolonthidae) Leonardo Delgado and Hector Castañeda | 456-459 |
| Contribution to the taxonomy of the Panamerican genus Fallceon (Ephemeroptera: Baetidae) <br> C. R. Lugo-Ortiz, W. P. McCafferty, and R. D. Waltz | 460-475 |
| A new species and new record of Catogenus Westwood from the Dominican Republic (Coleoptera: Passandridae) <br> Michael C. Thomas | 476-480 |
| Taxonomic names proposed in the insect order Heteroptera by José Candido de Melo Carvalho from January 1989 to January 1993 |  |
| José C. M. Carvalho and Richard C. Froeschner | 481-508 |
| Book Review |  |
| The Bee Genera of North and Central America (Hymenoptera: Apoidea) |  |
| Jerome G. Rozen, Jr. | 509-511 |
| Honorary, Life, and Sustaining Members | 512 |
| Reviewers for 1994 | 512 |
| Statement of Ownership, Management, and Circulation | 513 |

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The Journal of the New York Entomological Society publishes original research resulting from the study of insects and related taxa. Research that contributes information on taxonomy, classification, phylogeny, biogeography, behavior, natural history, or related fields will be considered for publication. 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.

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VOLUME $102 \quad$ OCTOBER $1994 \quad$ NO. 4

## CONTENTS

Natural history of leaf-folding caterpillars, Dichomeris spp. (Gelechiidae), on goldenrods and asters Carol C. Loeffler 405-428

A revision of the South American species of the ant genus Probolomyrmex (Hy-
menoptera: Formicidae)
Donat Agosti 429-434
Larval description of Abaris bigenera Bates, 1882, and notes on relationships of the genus Abaris Dejean, 1831 (Coleoptera: Carabidae: Pterostichini)

Yves Bousquet and James K. Liebherr
435-441
A review of the genus Pseudevoplitus Ruckes (Heteroptera: Pentatomidae), with the description of three new species

Jocélia Grazia, Miriam Becker, and Donald B. Thomas
442-455
A new species and new records of Cyclocephala from Guatemala (Coleoptera:
Melolonthidae)
Leonardo Delgado and Hector Castañeda 456-459
Contribution to the taxonomy of the Panamerican genus Fallceon (Ephemeroptera:
$\begin{array}{lll}\text { Baetidae) } & \text { C. R. Lugo-Ortiz, W. P. McCafferty, and R. D. Waltz } & 460-475\end{array}$
A new species and new record of Catogenus Westwood from the Dominican
Republic (Coleoptera: Passandridae)
Michael C. Thomas 476-480
Taxonomic names proposed in the insect order Heteroptera by José Candido de
Melo Carvalho from January 1989 to January 1993
José C. M. Carvalho and Richard C. Froeschner 481-508
Book Review
The Bee Genera of North and Central America (Hymenoptera: Apoidea)
Jerome G. Rozen, Jr.
509-511
Honorary, Life, and Sustaining Members 512
Reviewers for 1994512
Statement of Ownership, Management, and Circulation 513



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[^12]:    $\dagger$ Dr. Carvalho passed away October 21, 1994, after correcting and returning the manuscript.

