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REDESCRIPTION OF *PARACOCCUS MARGINATUS* WILLIAMS AND GRANARA DE WILLINK (HEMIPTERA: COCCOIDEA: PSEUDOCOCCIDAE), INCLUDING DESCRIPTIONS OF THE IMMATURE STAGES AND ADULT MALE

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Abstract.—*Paracoccus marginatus* Williams and Granara de Willink, commonly known as the papaya mealybug was first discovered in the Caribbean in 1994 and was collected in Florida in 1998. To facilitate implementation of control measures we have prepared descriptions, illustrations, and keys for all stages of this species including: First instar, second-instar male and female, third-instar male (prepupa) and female, fourth-instar male (pupa) and female (adult), and fifth-instar male (adult). Comparisons are given between *P. marginatus* and other species of *Paracoccus* as well as other commonly encountered mealybug species in Florida and the Caribbean.

Key Words: mealybugs, Coccoidea, Pseudococcidae, ontogeny, pest, papaya, *Carica papaya,* hibiscus, invasive species, pest, Florida, Caribbean

The genus *Paracoccus* includes some 79 species of varied distribution from the "Austro-Oriental, Ethiopian, Madagasian, Nearctic, Neotropical, New Zealand, Pacific, Palaearctic, and Oriental regions" (Ben-Dov 1994). Although most assigned species have not been recognized as major economic pests, there are two notable exceptions. *Paracoccus burnerae* (Brain) is considered a serious pest of citrus in South Africa (Hattingh 1993) and *Paracoccus marginatus* Williams and Granara de Willink has recently received attention as a pest of papaya and other economically important crops in the Caribbean and Florida.

Paracoccus marginatus or the papaya mealybug was originally reported from the Neotropical Region in Belize, Costa Rica, Guatemala, and Mexico (Williams and Granara de Willink 1992) and is believed to be native to at least part of Mexico and/or Central America (Miller et al. 1999). In 1993 or 1994, it was apparently introduced into the Caribbean Islands where it spread rapidly and is considered a pest of papaya in some areas (Miller et al. 1999). It has subsequently been reported from St. Martin (Matile-Ferrero and Étienne 1996) and Guadeloupe and St-Barthelemy Islands (Matile-Ferrero and Étienne 1998). Other Caribbean distribution records include: Antigua (Watson and Chandler 1999); Bahamas, San Salvador Island and New Providence (Watson, personal communication), Paradise Island (Meyerdirk, personal communication); British Virgin Islands (Watson and Chandler 1999); Cuba (Meyerdirk, personal communication); Dominican Republic (Meyerdirk, personal communication); Haiti (Meyerdirk, personal communication); Montserrat (Watson and Chandler 1999); Nevis (Watson and Chandler 1999);

Table 1. Host plants and references for *Paracoccus marginatus*.

Host Plant	Reference
Acacia sp.	Miller et al. (1999)
Acalypha sp.	Miller et al. (1999)
Acalypha wilkesiana Muell.-Arg.	Hamon (personal communication)
Ambrosia cumanensis auct. non Kunth	Williams and Granara de Willink (1992)
Annona squamosa L.	Miller et al. (1999)
Bauhinia sp.	Hamon (personal communication)
Carica papaya L.	Hamon (personal communication)
Carica sp.	Williams and Granara de Willink (1992)
Cestrum nocturnum L.	Hamon (personal communication)
Citrux x paradisi Macfad. (pro sp.)	Hamon (personal communication)
Clerodendrum paniculatum L.	Hamon (personal communication)
Coccoloba sp.	Miller et al. (1999)
Fistulosa sp.	Hamon (personal communication)
Guazuma ulmifolia Lam.	Miller et al. (1999)
Hamelia patens Jacq.	Hamon (personal communication)
Hamelia sp.	Hamon (personal communication)
Hibiscus sp.	Hamon (personal communication)
Hibiscus rosa-sinensis L.	Hamon (personal communication)
Ipomoea carnea Jacq.	Hamon (personal communication)
Ipomoea sp.	Miller et al. (1999)
Jatropha integerrima Jacq.	Hamon (personal communication)
Jatropha sp.	Hamon (personal communication)
Malvaviscus penduliflorus DC.	Hamon (personal communication)
Manihot chlorosticta Standl. & Goldman	Williams and Granara de Willink (1992), Miller et al. (1999)
Manihot esculenta Crantz	Williams and Granara de Willink (1992), Miller et al. (1999)
Mimosa pigra L.	Williams and Granara de Willink (1992)
Parthenium hysterophorus L.	Williams and Granara de Willink (1992), Miller et al. (1999)
Persea americana P. Mill.	Miller et al. (1999)
Plumeria rubra L.	Hamon (personal communication)
Plumeria sp.	Hamon (personal communication)
Rhaphiolepis umbellata (Thunb.) Makino	Hamon (personal communication)
Sida sp.	Williams and Granara de Willink (1992), Miller et al. (1999)
Solanum melongena L.	Miller et al. (1999)
Uniola paniculata L.	Hamon (personal communication)
Zea mays L.	Miller et al. (1999)

Puerto Rico (Meyerdirk, personal communication); St. Barthelemy (Meyerdirk, personal communication); St. Kitts (Watson and Chandler 1999); and U.S. Virgin Islands (Watson and Chandler 1999). Additionally, *P. marginatus* has recently been reported from French Guiana, South America (Matile-Ferrero et al. 2000). *Paracoccus marginatus* was first discovered in the United States in Manatee and Palm Beach counties, Florida in 1998 and has since been collected in Alachua, Brevard, Broward, Collier, Dade, Hillsborough, Manatee, Martin, Monroe, Palm Beach, Pinellas, Polk, Sarasota, and Volusia counties (Hamon, personal communication). Since its introduction into Florida, it has been collected 80 times in 30 different cities on 18 species of hosts. The species has apparently spread rapidly in the state.

Paracoccus marginatus has been reported from more than 25 genera of host plants including economically important crops such as papaya, citrus, yams, cassava, and hibiscus. Papaya mealybug hosts along with associated references are included in Table 1. Although this mealybug has also been recorded from many other hosts, these have yet to be confirmed and are not included in Table 1.

Williams and Granara de Willink (1992) published the first taxonomic paper on *Paracoccus marginatus* and included a description and illustration of the adult female. They also provided descriptions and a key for the 21 species of *Paracoccus* occurring in Central and South America. The purpose of this research is to describe and illustrate all instars (including the adult male and female) of this potentially serious invasive species in order to facilitate its recognition as part of any control initiatives that may be undertaken.

METHODS

Terminology in the descriptions follows that of Williams and Granara de Willink (1992) and Gimpel and Miller (1996) for adult females and immatures and that of Afifi (1968) for adult males. Measurements were made with an ocular micrometer using a Leica DMRB compound microscope. Numbers and measurements are from 10 specimens and are given as an average followed by the range in parentheses. Associated enlargements of various structures on the illustrations are not proportional. All specimens studied are from the National Museum of Natural History, Coccoidea Collection, Beltsville, MD. Information listed in the SPECIMENS EXAMINED section is verbatim from information recorded on the microscope slides. The abbreviation "ad." refers to adult specimens.

Tables 3–6 contain 12 of the most common mealybugs in the Caribbean region and were selected for comparison to *P. marginatus.* Included species are: *Dysmicoccus brevipes* (Cockerell); *Ferrisia virgata* (Cockerell); *Maconellicoccus hirsutus* (Green); *Nipaecoccus nipae* (Maskell); *Phenacoccus gossypii* Townsend and Cockerell; *Phenacoccus madeirensis* Green; *Phenacoccus solenopsis* Tinsley; *Planococcus citri* (Risso); *Planococcus minor* (Maskell); *Pseudococcus jackbeardsleyi* Gimpel and Miller; *Pseudococcus longispinus* (Targioni Tozzetti); and *Pseudococcus viburni* (Signoret). *Phenacoccus gossypii* and *P. madeirensis* are listed together as are *Planococcus citri* and *P. minor* because of morphological similarities. There are other species of *Phenacoccus, Pseudococcus,* and *Nipaecoccus* that could be included in this list, but they are also so similar in general appearance to other species in the genus that characters of one species in the genus are sufficient to distinguish all species in the immature instars.

Host plant names included in Table 1 were verified in Integrated Taxonomic Information System (Anonymous 2001).

RESULTS

Paracoccus marginatus
Williams and Granara de Willink

Suggested Common Name:
Papaya mealybug
(Figs. 1–8)

KEY TO INSTARS

1. Without wings or wing buds on thorax . . . 4
– With wings or wing buds on thorax 2
2(1). Genitalia weakly sclerotized, aedeagus absent; wings represented by buds less than ½ length of body, without a vein 3
– Genitalia heavily sclerotized, aedeagus apparent; wings approximately as long as body, with small basal vein (Fig. 8) . . . . adult male
3(2). Antenna unsegmented; wing buds small, less than length of thorax; head without sclerotization (Fig. 6) . . . . prepupal male
– Antenna with 10 segments; wing buds large, about same length as thorax; head with weak sclerotization (Fig. 7) . . . . . pupal male
4(1). Antennae 6-segmented 5
Antennae with 7 or 8 segments 8
5(4). Without tubular ducts or with less than 5 such ducts 6
With more than 5 tubular ducts particularly on dorsal abdomen (Fig. 5) . . . . second-instar male
6(5). Third antennal segment with more than 4 setae; anal-lobe cerarius with at least 1 auxiliary seta 7
– Third antennal segment with 4 setae; anal-lobe cerarius without auxiliary setae (Fig. 4) . . . . first instar
7(6). Third antennal segment with 5 setae; tibia divided by tarsus 0.9(0.8–1.0) (Fig. 3) . . . . second-instar female
– Third antennal segment with 9 setae; tibia

divided by tarsus 1.2(1.2–1.4) (Fig. 2) . . .
. . . . third-instar female (in part)
8(4). Antenna 7-segmented; with less than 5 multilocular pores; without vulva (Fig. 2) . . .
. . . . third-instar female (in part)
– Antenna 8-segmented; with more than 5 multilocular pores; with vulva (Fig. 1) . . .
. . . . adult female

Type data.—We have not examined type material of this species, but have studied many of the specimens that were used in the original description but were not included in the type series.

Etymology.—The species epithet is derived from a Latin word meaning enclosed within a border and refers to the border of oral rim tubular ducts (Williams and Granara de Willink 1992).

ADULT FEMALE
(Fig. 1)

Field features.—Body yellow, dusted with mealy wax not thick enough to hide body color, without discrete bare areas on dorsum, with many short waxy filaments around body margin. Ovisac developed beneath and behind adult female.

Slide-mounted characters.—Body 2.2(1.5–2.7) mm long, 1.4(0.9–1.7) mm wide.

Dorsum with 16(14–17) pairs of cerarii; cerarii 1, 2, 4, 5, 7, and 9 with 2 conical setae (Fig. 1M); cerarii 3, 6, and 16 with 3(2–3) conical setae; cerarii 8, 11, and 17 with 2(0–2); cerarii 10 and 14 with 1(0–2) conical setae; cerarii 12, 13, and 15 with 2(0–3) conical setae. Cerarius 12 without auxiliary setae, with 2(0–3) conical setae, 5(0–8) trilocular pores, 1(0–3) discoidal pores. Anal-lobe cerarius (Fig. 1I) with 1(1–3) auxiliary setae (Fig. 1J), 2 conical setae, 13(10–18) trilocular pores (Fig. 1C), 2(0–3) discoidal pores (Fig. 1K). Dorsal body setae (Fig. 1L) more slender than cerarian setae. Multilocular pores absent; trilocular pores scattered over surface, most abundant near setae; discoidal pores rare, about ½ diameter of trilocular pore. Oral-rim tubular ducts (Fig. 1B) usually restricted to marginal areas associated with cerarii, 1 specimen examined with 1 mediolateral duct on segment I and 1 in medial area of mesothorax; of 21 specimens examined cerarius 1 without associated oral rim, cerarius 2 with associated oral rim in 20 of 21 specimens, cerarius 3 with 4 on 21 specimens, cerarius 4 with 12 on 21, cerarius 5 with 11 on 21, cerarius 6 with 17 on 21, cerarius 7 with 18 on 21, cerarius 8 with 20 on 21, cerarii 9 and 10 without associated oral rims, cerarius 11 with 15 on 21, cerarius 12 with 4 on 21, cerarii 13, 15, and 16 without associated oral rim, cerarius 14 with 2 on 21, and cerarius 17 with 15 oral rims on 21 specimens. Oral-collar tubular ducts absent. Longest submedial seta on segment VII 10(8–14) μ long; 1(0–2) submedial setae on segment VIII, when present longest seta 13(8–18) μ long.

Anal-ring seta 136(120–150) μ long; 1.4(1.2–1.7) times as long as width of anal ring.

Venter with multilocular pores (Fig. 1G) usually in posterior and anterior bands on segments VI–VIII and restricted to posterior band on segments IV and V, 1 or 2 specimens with 1 or 2 pores on segment III or with a few pores on anterior margins of segments IV and V; 3 of 10 specimens with 1 multilocular pore near base of front or hind leg. Trilocular pores concentrated near setal bases. Discoidal pores uncommon, of same size as on dorsum. Oral-rim tubular ducts in mediolateral areas from prothorax to segment I, with 4(3–6) ducts on each side of body. Oral-collar tubular ducts of 1 size, in conspicuous marginal clusters along body margin from segments II–VII, often with 2 or 3 pores on segment I, also present in medial and mediolateral areas of abdominal segments III–VIII, present on thorax in seta clusters near hind 2 pairs of legs, occasionally with 1 or 2 along body margin of thorax especially in area laterad of anterior spiracle and front legs, absent from head. Setae as follows: 4 cisanal (Fig. 1H), longest 52(45–68) μ long; longest anal-lobe seta 170(155–200) μ long; longest seta on trochanter 104(95–110) μ long. Anal-lobe

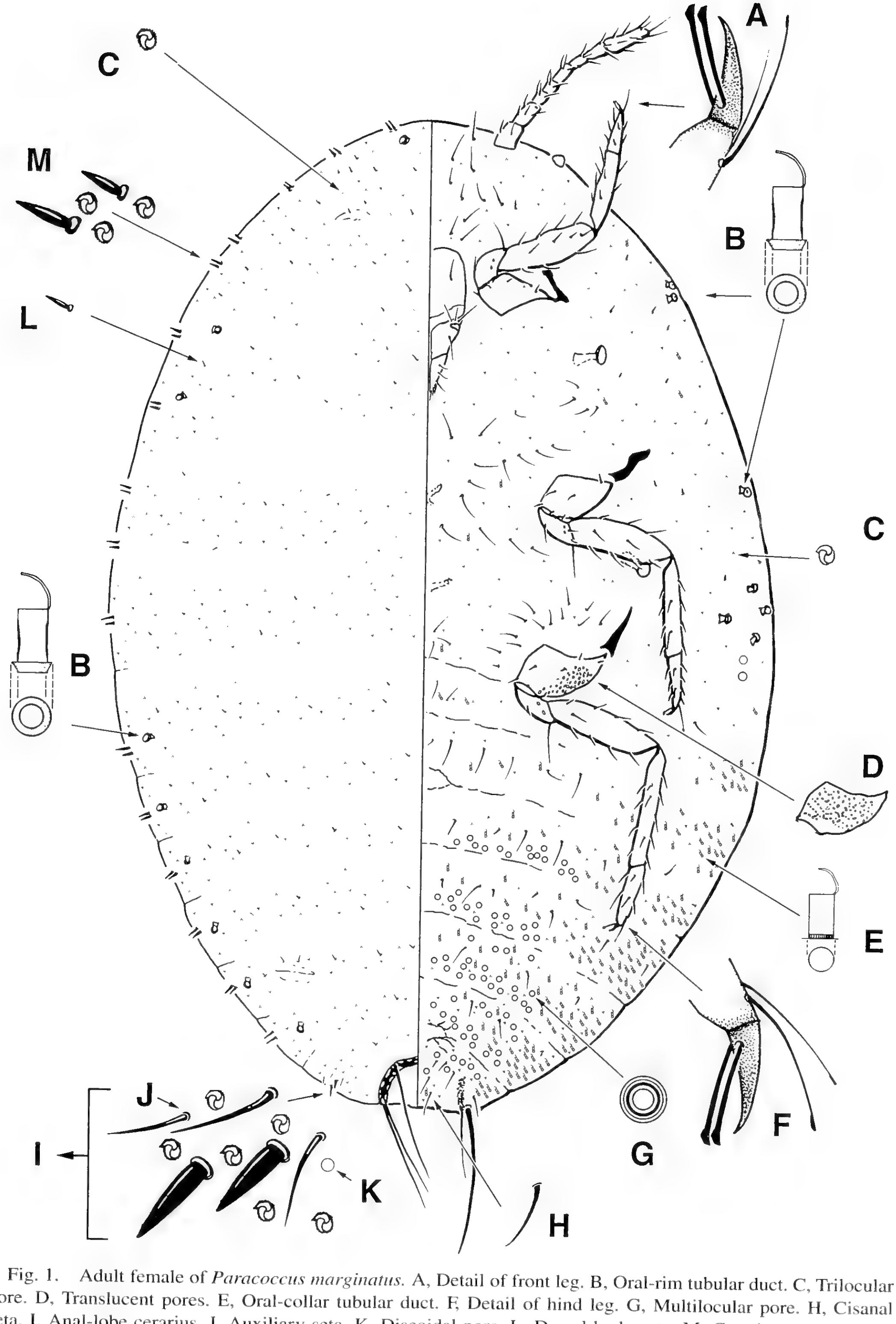

Fig. 1. Adult female of *Paracoccus marginatus*. A, Detail of front leg. B, Oral-rim tubular duct. C, Trilocular pore. D, Translucent pores. E, Oral-collar tubular duct. F, Detail of hind leg. G, Multilocular pore. H, Cisanal seta. I, Anal-lobe cerarius. J, Auxiliary seta. K, Discoidal pore. L, Dorsal body seta. M, Cerarian seta.

bar conspicuously wider than base of anal bar seta.

Circulus 60(49–80) μ wide, generally divided by intersegmental line. Labium 137(125–162) μ long. Antenna 8-segmented, 372(335–400) μ long. Legs with translucent pores restricted to hind coxa, ventral surface (when leg is lying flat as shown in illustration) with 40(14–62) pores, dorsal surface (Fig. 1D) with 79(54–108) pores. Hind femur 209(195–225) μ long; hind tibia 211(185–228) μ long; hind tarsus 94(91–100) μ long. Hind tibia/tarsus 2.2(2.0–2.3); hind femur/tarsus 1.0(0.9–1.1). Length of hind femur divided by greatest width of hind femur 3.7(3.0–4.2). Hind tibia with 15(14–19) setae. Claw digitules on all legs clubbed, approximately same size. Tarsal digitules (Fig. 1F) on hind 2 pairs of legs clubbed, each tarsus with 1 digitule noticeably longer and with club slightly larger than other; tarsal digitules (Fig. 1A) on front pair of legs of 2 different sizes and shapes, 1 digitule on each tarsus clubbed and robust, other digitule without club, slender.

Notes.—The above description is based on 240 specimens from 41 localities. The adult female can be distinguished from all other instars by having multilocular pores, translucent pores on hind coxa, and a vulva.

THIRD-INSTAR FEMALE
(Fig. 2)

Slide-mounted characters.—Body 1.1(0.7–1.8) mm long, 0.7(0.3–1.1) mm wide.

Dorsum with 6(1–10) pairs of cerarii; cerarii indefinite, when present, with 2 conical setae and 1 trilocular pore between conical setae. Cerarius 12 absent. Anal-lobe cerarius with 1(1–2) auxiliary setae, 2 conical setae, 5(4–7) trilocular pores, 0(0–1) discoidal pores. Dorsal body setae more slender than cerarian setae. Multilocular pores absent; trilocular pores scattered over surface, most abundant near setae; discoidal pores rare, about ½ diameter of trilocular pore. Oral-rim tubular duct rarely present near position of cerarius 8 (of 10 specimens examined, 4 had 1 oral rim or large oral collar on at least one side of body). Oral-collar tubular ducts absent. Longest submedial seta on segment VII 7(5–10) μ long; 1(0–2) submedial setae on segment VIII, when present longest seta 7(5–9) μ long.

Anal-ring seta 87(78–92) μ long; 1.6(1.3–1.8) times as long as width of anal ring.

Venter with multilocular pores absent (present on 1 of 10 specimens examined, restricted to segment VIII). Trilocular pores concentrated near setal bases. Discoidal pores uncommon, of same size as on dorsum. Oral-rim tubular ducts sometimes present near body margin on abdominal segment II, III, or on metathorax (of 10 specimens examined, 4 had 1 or 2 oral rims or large oral collar on at least one side of body). Oral-collar tubular ducts absent. Setae as follows: 4 cisanal, longest 33(22–50) μ long; longest anal-lobe seta 132(112–158) μ long; longest seta on trochanter 63(50–85) μ long. Anal-lobe bar slightly narrower than on adult female.

Circulus 47(22–80) μ wide, generally divided by intersegmental line. Labium 85(70–100) μ long. Antenna 6- or 7-segmented (of 10 specimens examined 5 had 6-segments with weak indication of partial division between segments 3 and 4), when 6-segmented, segment 3 with 9 setae, 233(205–262) μ long. Legs without translucent pores. Hind femur 114(100–138) μ long; tibia 108(98–127) μ long; tarsus 84(80–90) μ long. Hind tibia/tarsus 1.2(1.2–1.4); hind femur/tarsus 1.1(1.0–1.2). Length of hind femur divided by greatest width of hind femur 2.5(2.0–3.1). Hind tibia with 9(7–10) setae. Claw and tarsal digitules same as on adult female except sometimes 1 claw digitule slightly smaller that other.

Notes.—The above description is based on 42 specimens from 12 localities. The third-instar female can be distinguished from all other instars by having 6- or 7-segmented antennae, when 6-segmented with

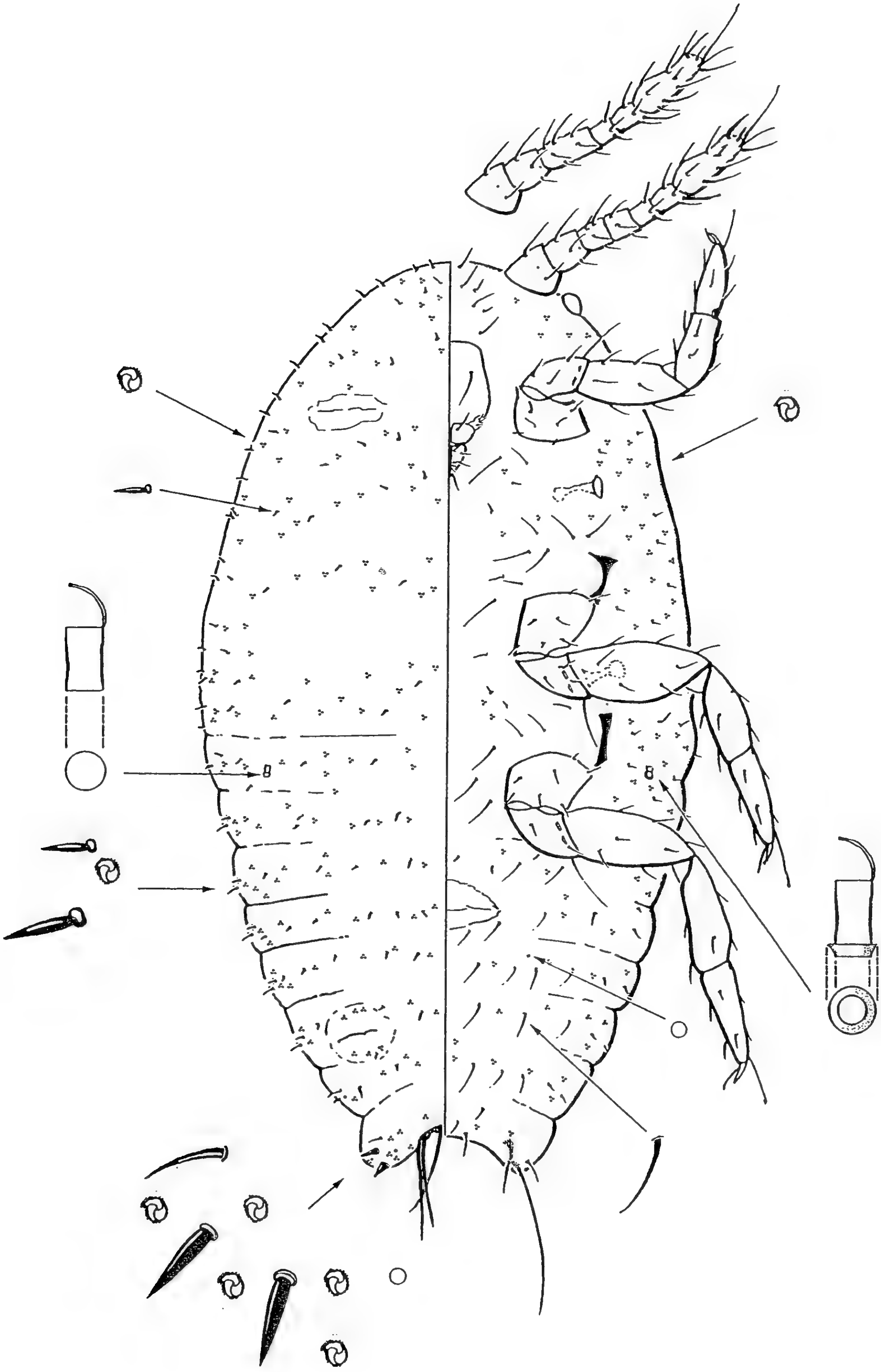

Fig. 2. Third-instar female of *Paracoccus marginatus*.

hind tibia divided by hind tarsus length usually 1.2, and about 9 setae on the hind tibia.

Second-instar Female
(Fig. 3)

Field features.—Body color yellow.

Slide-mounted characters.—Body 0.7(0.5–0.8) mm long, 0.4(0.3–0.5) mm wide.

Dorsum with 6(4–11) pairs of cerarii; cerarii indefinite, when present, with 2 conical setae and 1 trilocular pore between conical setae. Cerarius 12 absent. Anal-lobe cerarius with 1 auxiliary setae, 2 conical setae, 2(2–3) trilocular pores, sometimes with 1 discoidal pore. Dorsal body setae more slender than cerarian setae. Multilocular pores absent; trilocular pores scattered over surface, most abundant near setae; discoidal pores rare, about ½ diameter of trilocular pore. Oral-rim tubular ducts absent. Oral-collar tubular ducts absent. Longest submedial seta on segment VII 6(5–6) μ long; without submedial setae on segment VIII.

Anal-ring seta 60(52–70) μ long; 1.5(1.3–1.8) times as long as width of anal ring.

Venter with multilocular pores absent. Trilocular pores concentrated near setal bases, absent in medial area of abdomen. Discoidal pores rare. Oral-rim tubular ducts absent. Oral-collar tubular ducts absent. Setae as follows: 4 cisanal, longest 20(18–25) μ long; longest anal-lobe seta 95(88–102) μ long; longest seta on trochanter 49(42–55) μ long. Anal-lobe bar narrower than on adult female.

Circulus 40(20–75) μ wide, generally divided by intersegmental line. Labium 69(62–75) μ long. Antenna 6-segmented, 173(152–185) μ long; antennal segment 3 with 5 setae. Legs without translucent pores. Hind femur 78(72–82) μ long; hind tibia 66(58–72) μ long; hind tarsus 69(65–72) μ long. Hind tibia/tarsus 0.9(0.8–1.0); hind femur/tarsus 1.2(1.1–1.3). Length of hind femur divided by greatest width of hind femur 2.3(2.1–2.5). Hind tibia with 9(8–9) setae. Claw and tarsal digitules same as on adult female except 1 claw digitule conspicuously smaller on all legs.

Notes.—The above description is based on 64 specimens from 9 localities. The second-instar female can be distinguished from all other instars by lacking oral-collar tubular ducts and multilocular pores, and by having 5 setae on the third antennal segment.

First Instar (Gender Not Determined)
(Fig. 4)

Slide-mounted characters.—Body 0.4(0.3–0.5) mm long, 0.2(0.2–0.3) mm wide.

Dorsum with 9(7–10) pairs of cerarii; cerarii indefinite, when present, with 2 conical setae and 1 trilocular pore between conical setae. Cerarius 12 absent. Anal-lobe cerarius without auxiliary setae, 2 conical setae, 1 trilocular pore, without discoidal pores. Dorsal body setae more slender than cerarian setae. Multilocular pores absent; trilocular pores scattered over surface, forming 2 longitudinal lines on each side of abdomen, excluding cerariian setae. Discoidal pores absent. Oral-rim tubular ducts absent. Oral-collar tubular ducts absent. Longest submedial seta on segment VII 5(4–8) μ long; without submedial setae on segment VIII.

Anal-ring seta 37(30–42) μ long; 1.4(1.2–1.6) times as long as width of anal ring.

Venter without multilocular pores. Trilocular pores restricted to 10 positions on each side of body on head, thorax, and anterior abdomen (see Fig. 4 for position labels); triloculars in positions 1 to 7 and 10 rarely absent, pores in positions 8 and 9 often absent. Discoidal pores in submarginal line on each side of abdomen, usually with 1 pore posterior of each spiracle. Oral-rim and oral-collar tubular ducts absent. Setae as follows: 4 cisanal, longest 17(12–22) μ long; longest anal-lobe seta 58(45–69) μ long; longest seta on trochanter 38(35–42) μ long. Anal-lobe bar narrower than on adult female.

Circulus 37(20–55) μ wide, generally di-

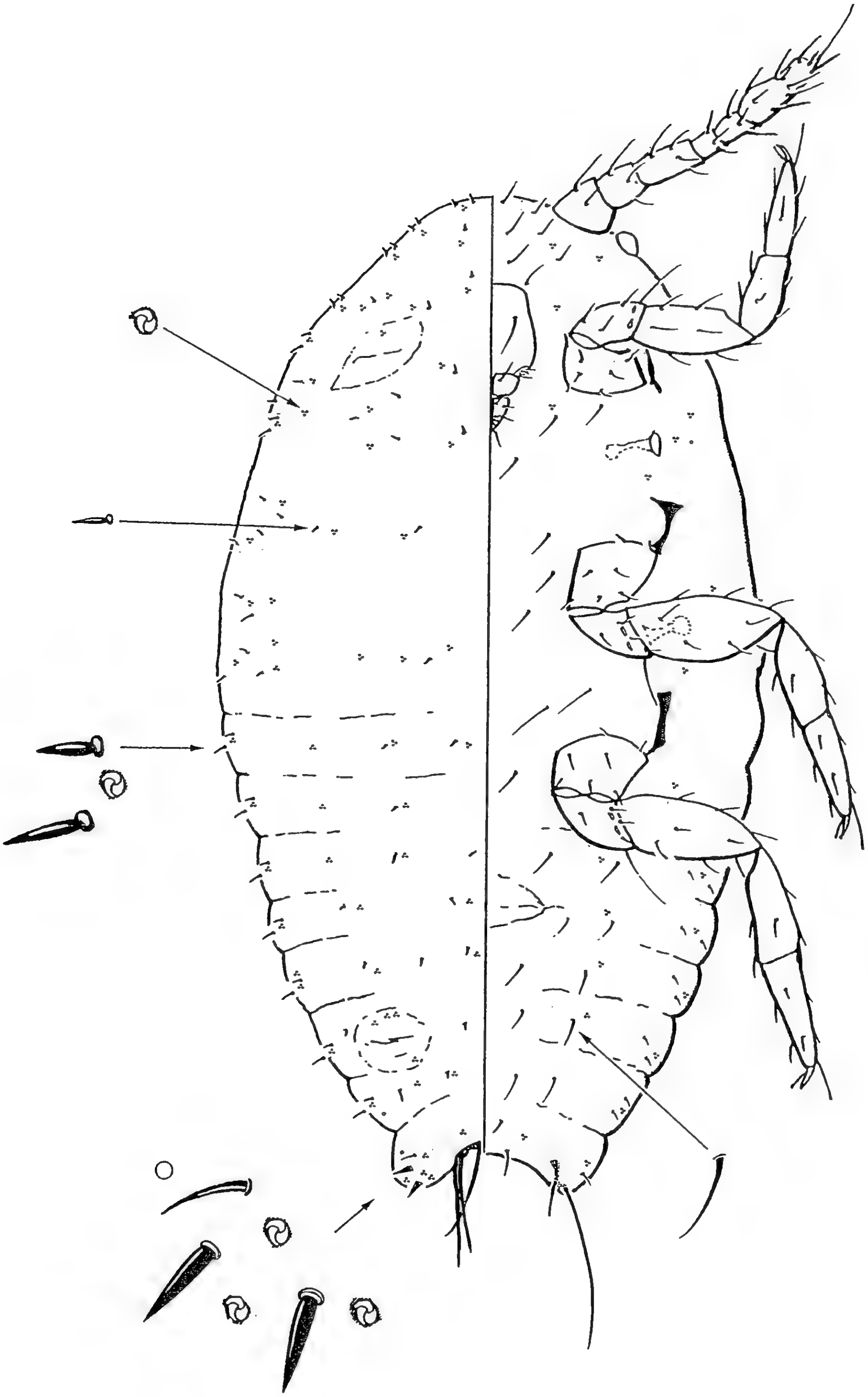

Fig. 3. Second-instar female of *Paracoccus marginatus*.

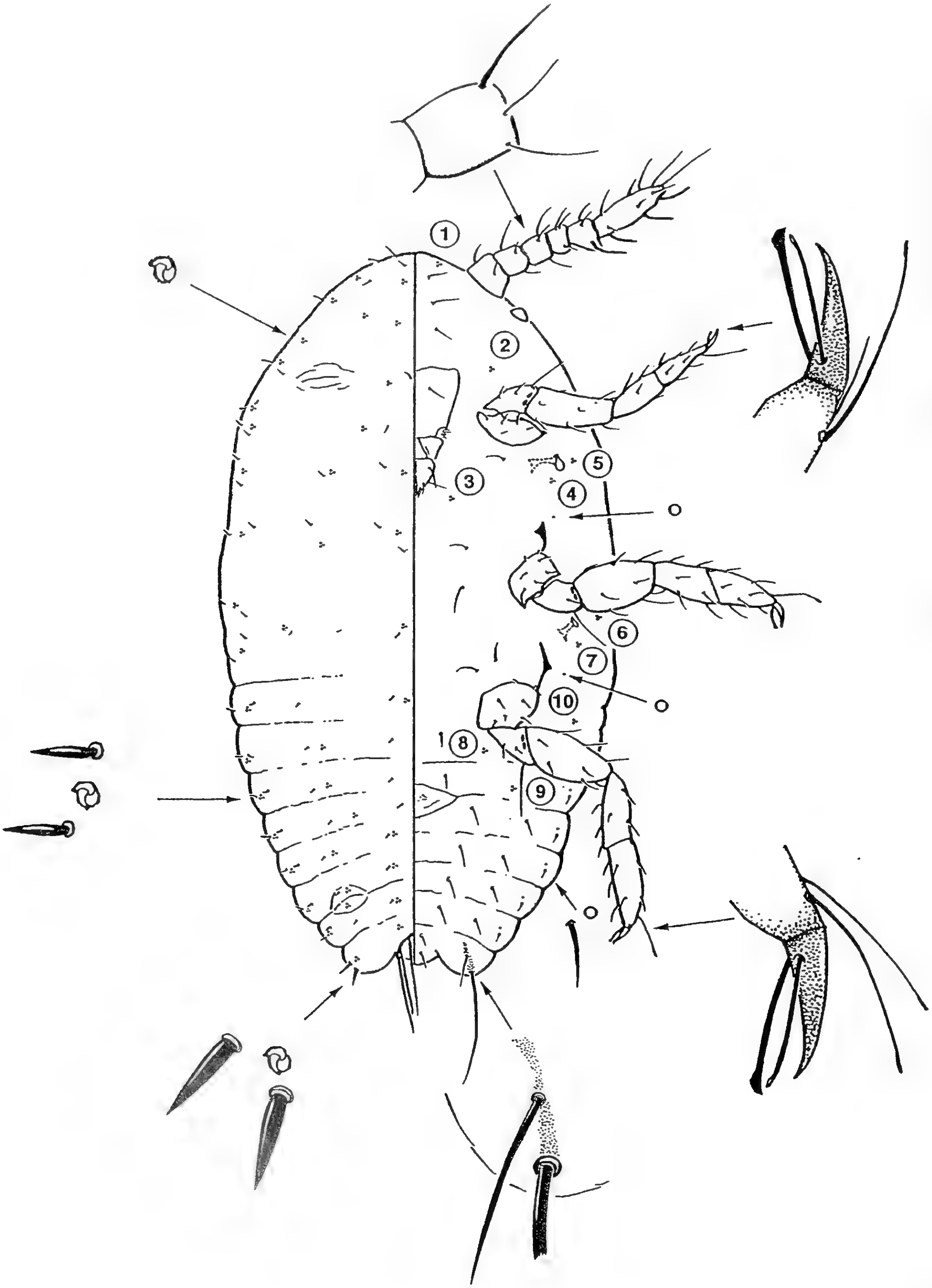

Fig. 4. First-instar of *Paracoccus marginatus*, gender not determined. Numbers refer to positions of ventral trilocular pores.

vided by intersegmental line. Labium 48(44–52) μ long. Antenna 6-segmented, 132(120–148) μ long; antennal segment 3 with 4 setae. Legs without translucent pores. Hind femur 59(55–62) μ long; hind tibia 50(45–55) μ long; hind tarsus 57(53–62) μ long. Hind tibia/tarsus 0.9(0.8–0.9); hind femur/tarsus 1.2(1.1–1.3). Length of hind femur divided by greatest width of hind femur 2.3(1.8–2.5). Hind tibia with 9 setae. Claw and tarsal digitules same as on adult female except 1 claw digitule conspicuously smaller on all legs.

Notes.—The above description is based on 86 specimens from 6 localities. The first-instar can be distinguished from all other instars by having no auxiliary setae in the anal-lobe cerarius, 2 longitudinal lines of trilocular pores on dorsal abdomen on each side of body (excluding cerariian setae), and antennal segment 3 with 4 setae.

SECOND-INSTAR MALE
(Fig. 5)

Field features.—Body color usually pink, occasionally yellow.

Slide-mounted characters.—Body 0.6(0.5–1.0) mm long, 0.3(0.2–0.6) mm wide.

Dorsum with 4(2–5) pairs of cerarii; cerarii indefinite, when present, with 2 conical setae and 1 trilocular pore between conical setae. Cerarius 12 absent. Anal-lobe cerarius with 1(1–2) auxiliary setae, 2 conical setae, 2(2–3) trilocular pores, without discoidal pores. Dorsal body setae more slender than cerarian setae. With 1(0–2) multilocular pores in medial areas of thorax and/or head, present on 6 of 10 specimens examined; trilocular pores scattered over surface, most abundant near setae; discoidal pores rare, about ½ diameter of trilocular pore. Oral-rim tubular ducts absent. Oral-collar tubular ducts abundant over surface, of 1 size. Longest submedial seta on segment VII 6(5–8) μ long; without submedial setae on segment VIII.

Anal-ring seta 54(48–58) μ long; 1.3(1.2–1.5) times as long as width of anal ring.

Venter with multilocular pores mesad of each pair of legs, for hind pair of legs located on segment III, with 4(2–5) pores on body. Trilocular pores concentrated near setal bases. Discoidal pores rare. Oral-rim tubular ducts absent. Oral-collar tubular ducts of 2 sizes: larger size same as on dorsum, located marginally; smaller size present in longitudinal line along submargin of abdomen. Setae as follows: 4 cisanal, longest 21(17–26) μ long; longest anal-lobe seta 91(83–108) μ long; longest seta on trochanter 47(40–55) μ long. Anal-lobe bar narrower than on adult female.

Circulus 50(40–75) μ wide, generally divided by intersegmental line. Labium 67(62–72) μ long. Antenna 6-segmented, 171(160–188) μ long; antennal segment 3 with 5 setae. Legs without translucent pores. Hind femur 82(75–92) μ long; hind tibia 68(61–80) μ long; hind tarsus 62(52–70) μ long. Hind tibia/tarsus 1.1(1.0–1.2); hind femur/tarsus 1.2(1.1–1.4). Length of hind femur divided by greatest width of hind femur 2.6(2.2–3.0). Hind tibia with 9(8–9) setae. Claw and tarsal digitules same as on adult female except 1 claw digitule conspicuously smaller on all legs.

Notes.—The above description is based on 86 specimens from 7 localities. The second-instar male can be distinguished from all other instars by having dorsal oral-collar tubular ducts and multilocular pores near 1 or more pairs of legs. In addition, live and alcohol preserved specimens tend to appear more narrowly elongate than other associated second-instar females, third-instar females, or first instars.

Both field collected and laboratory reared early instars of *P. marginatus* exhibit pink and yellow forms. We hypothesize that the pink forms are males. Pink forms were collected in the field on St. Kitts, W.I. In addition, Richard Warkentin (USDA, APHIS-PPQ, Biological Control Technical Specialist) collected and sorted a vial of pink specimens and a vial of yellow ones from the Papaya mealybug rearing facilities in St. Thomas, U.S.V.I. However, the results from

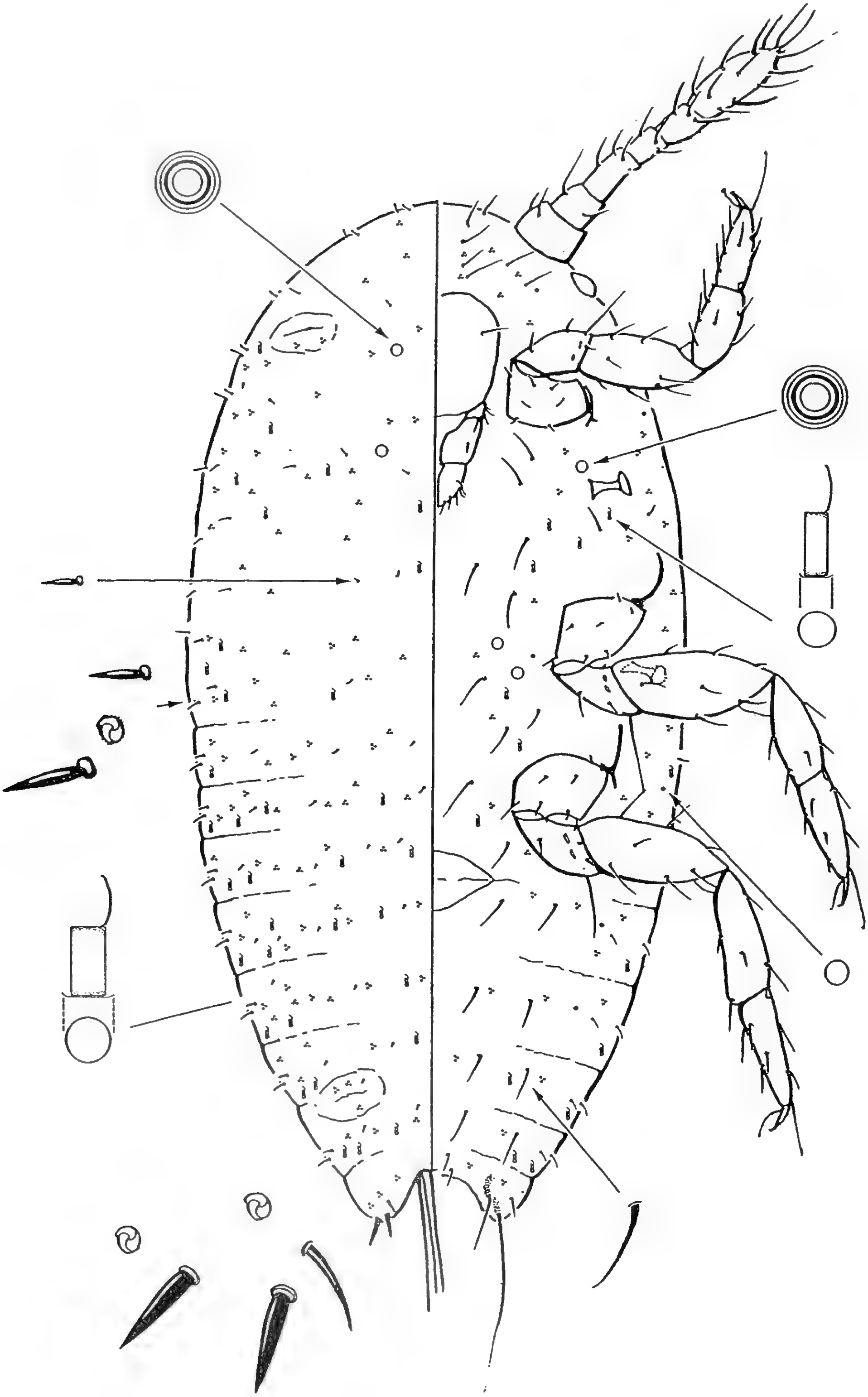

Fig. 5. Second-instar male of *Paracoccus marginatus.*

both collection sites were inconclusive. Although field collected pink forms were mostly second instar males, there were a few second instar females present. Results of the laboratory reared specimens were also inconclusive. While specimens of the pink form yielded only second instar males, specimens of the yellow form yielded both second instar males and second instar females although there were many more females than males. Contamination, especially for field collected specimens may be a possibility for the discrepancies but, this is probably unlikely for the specimens collected at the rearing facilities.

THIRD-INSTAR MALE (PREPUPA)
(Fig. 6)

Slide-mounted characters.—Body 0.9(0.8–1.1) mm long, 0.4(0.3–0.4) mm wide.

Dorsum without cerarii; posterolateral margins of segments V, or VI, VII, and VIII each with 2 setae conspicuously longer than remaining setae on abdominal segments. Multilocular pores in medial areas of head, forming row on prothorax and metathorax, usually without pores on mesothorax, occasionally with 1 or 2 medially, in rows on most abdominal segments, fewer in medial area, absent from segments VIII and IX; trilocular pores absent; discoidal pores rare. Oral-rim tubular ducts absent. Oral-collar tubular ducts present around body margin, medial and submedial ducts sometimes present on prothorax, metathorax and 1 or 2 abdominal segments. Longest submedial seta on segment VII 18(15–20) μ long; without submedial setae on segment VIII.

Anal-ring setae absent; anal ring 25(20–28) μ wide.

Venter with multilocular pores near anterior margin on head, near spiracles, legs, and in medial areas of pro- and mesothorax on thorax, in rows on abdominal segments, sparse medially, absent from segments VIII and IX. Trilocular pores absent. Discoidal pore located near each pair of legs. Oral-rim tubular ducts absent. Oral-collar tubular ducts restricted to margin. Longest anal-lobe seta 67(50–78) μ long.

Circulus appearing collapsed, 62(45–98) μ wide, resting on intersegmental line. Labium absent. Antennal segments indistinct, 226(215–248) μ long. Hind femur 90(82–95) μ long; division between hind tibia and tarsus indistinct, hind tibia + tarsus 134(130–140) μ long. Length of hind femur divided by greatest width of hind femur 2.7(2.2–3.0). Wing buds of mesothorax protruding from lateral margin, 67(50–78) μ long. Hamulohalterae represented by small swelling on lateral margin of metathorax.

Notes.—The above description is based on 16 specimens from 3 localities. The prepupa can be distinguished from all other instars by having multilocular pores, oral-collar tubular ducts, antennae without definite segmentation, tibia + tarsus fused, no labium, no aedeagus, and no definite constriction for the head.

FOURTH-INSTAR MALE (PUPA)
(Fig. 7)

Slide-mounted characters.—Body 1.0(0.9–1.0) mm long, 0.3(0.3–0.4) mm wide.

Dorsum without cerarii; posterolateral margins of segments III, IV, or V, to segment VIII each with 2 setae conspicuously longer than remaining setae on abdominal segments. Multilocular pores absent from head, forming conspicuous row on prothorax, mediolateral cluster on metathorax, without pores on mesothorax, in mediolateral clusters on each side of abdominal segments I–VI or VII; trilocular pores absent; discoidal pores associated with multiloculars and oral collars. Oral-rim tubular ducts absent. Oral-collar tubular ducts present near body margin of prothorax and abdominal segments I or II to VII or VII, forming clusters of 2(1–5) ducts. Longest submedial seta on segment VII 20(16–28) μ long; without submedial setae on segment VIII.

Anal-ring setae absent; anal ring 27(25–30) μ wide.

Venter with multilocular pores absent

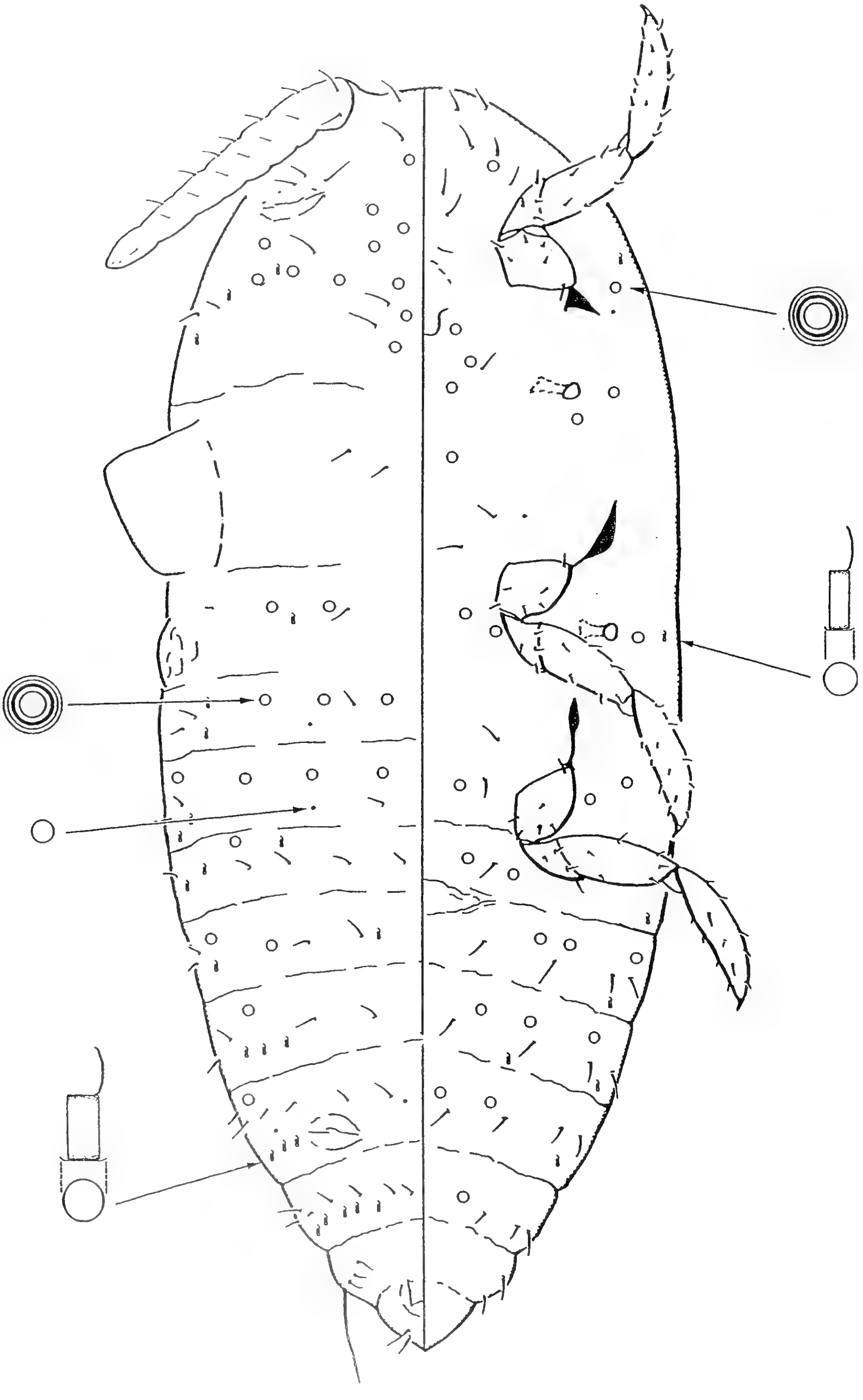

Fig. 6. Third-instar male or prepupa of *Paracoccus marginatus*.

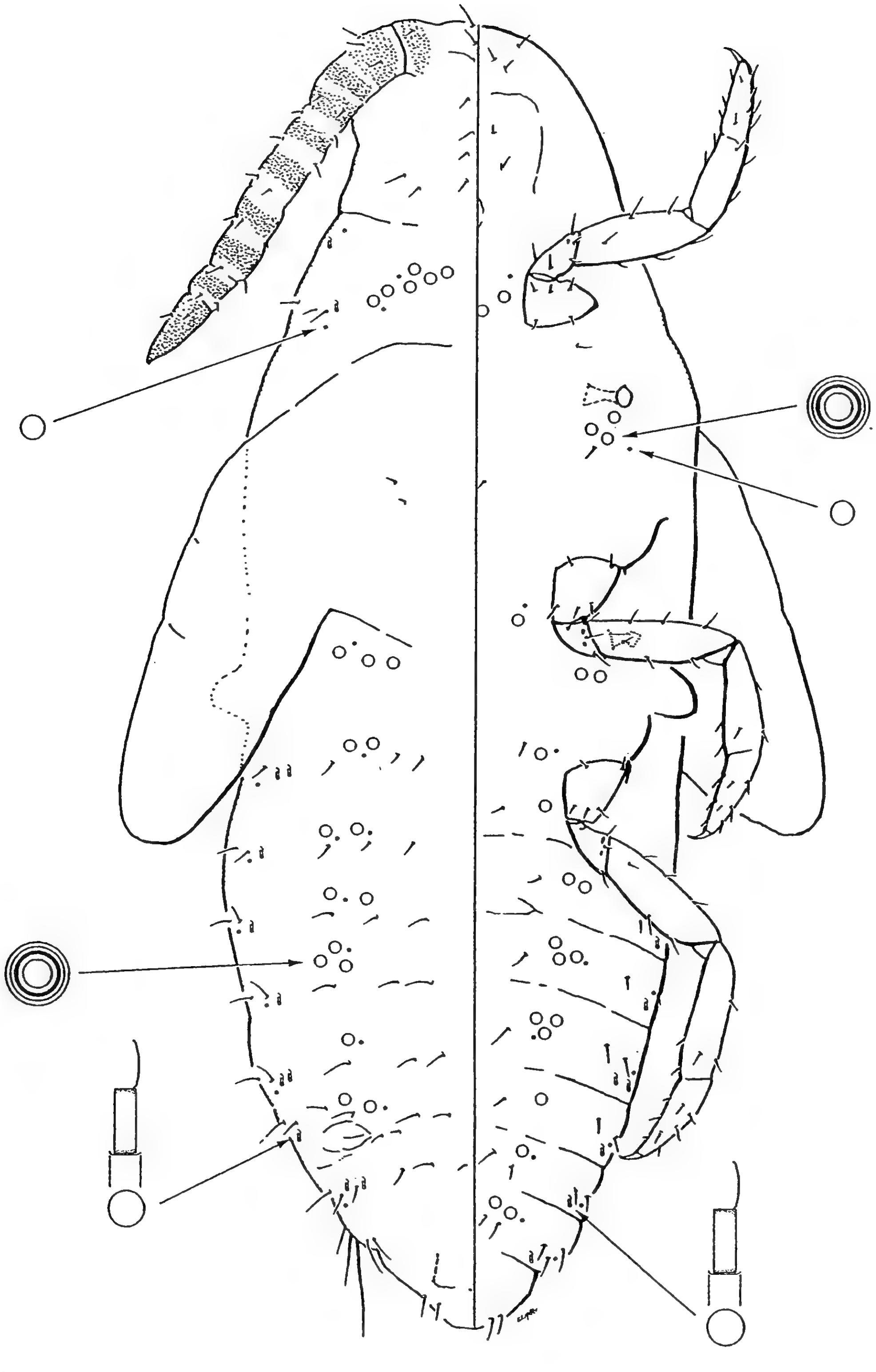

Fig. 7. Fourth-instar male or pupa of *Paracoccus marginatus*.

from head, row of pores between front coxae, present on remainder of thorax near spiracles and legs, in mediolateral clusters of 2(1–4) pores on each side of segments II–VI, VII, or VIII. Trilocular pores absent. Discoidal pores associated with oral-collars and multiloculars. Oral-rim tubular ducts absent. Oral-collar tubular ducts present near body margin of prothorax usually forming cluster of several ducts, sometimes absent from abdomen or with 1 duct near body margin on each of abdominal segments II–VII or VIII. Longest anal-lobe seta 60(48–72) μ long.

Circulus ill-defined. Labium absent. Antenna 10-segmented, 357(345–375) μ long. Hind femur 109(105–115) μ long; hind tibia 111(105–112) μ long; hind tarsus 80(75–88) μ long. Hind tibia/tarsus 1.4(1.3–1.5); hind femur/tarsus 1.0. Length of hind femur divided by greatest width of hind femur 3.3(3.2–3.4). Wing buds of mesothorax protruding from lateral margin, 336(250–385) μ long. Hamulohalterae 36(22–42) μ long.

Notes.—The above description is based on 8 specimens from 1 locality. The pupa can be distinguished from all other instars by having multilocular pores, oral-collar tubular ducts, 10 segmented antennae, no labium, no aedeagus, and a slight constriction between the thorax and head.

ADULT MALE
(Fig. 8)

Slide-mounted characters.—Body elongate oval, 1.0(0.9–1.1) mm long; greatest width at thorax 0.3(0.2–0.3) mm.

Dorsum with 1 pair of tail-forming pore clusters; each cluster with 2 elongate setae approximately 250 μ long, 1 sometimes 2 additional shorter setae, 38(34–42) multilocular pores, and 1 or 2 discoidal pores. Multilocular pores in marginal areas of prothorax and each abdominal segment, with 5(3–7) on each side of segment I, 2(1–3) on each side of segment II, 2(1–2) on III, 2(1–3) on IV, 2(1–3) on V, 2(1–3) on VI, 1(1–2) on each side of segment VII, multilocular pores with 4 or 5 loculi, quinqueloculars predominate (Fig. 8G); normally without pores on head (1 of 10 specimens with 1 pore near lateral arm of midcranial ridge). Discoidal pores (Fig. 8F) associated with lateral abdominal multilocular pores. Body setae bristle shaped. Small abdominal tergites present on mid-dorsum of segments I–III and dorsum of segment VIII. Dorsal abdominal tergites usually without associated setae. Metapostnotal ridge conspicuous. Scutellum rectangular, with several medial setae. Scutum sclerotized throughout except for a median longitudinal clear area which bears several setae. Prescutum rectangular with well defined prescutal ridge, weakly defined prescutal suture and several setae. Pronotal ridge heavily sclerotized. Hamulohalterae 75(67–82) μ long, with 1 apical hooked seta. Mesothoracic wings 932(889–988) μ long, each with 2–3 basal setae. Head width 180(148–193) μ; dorsal eye 34(30–40) μ in diameter, lateral ocellus 17(12–20) μ in diameter and located at junction of preocular and postocular ridges. Dorsal arm of midcranial ridge (Fig. 8A) extending beyond posterior margin of dorsal eye. Median crest weakly sclerotized with several setae. Ocular sclerite weakly sclerotized.

Penial sheath (Fig. 8C and 8E) 95(86–106) μ long, 70(62–74) μ wide with distinct ventral lobes; length/width ratio 1.4. Aedeagus (Fig. 8D) 68(54–79) μ long, broad and apically truncate.

Venter with hair-like setae only, present medially, submedially and laterally of most abdominal segments as well as few scattered prosternal and basisternal setae. Abdominal sclerotization confined to segment VIII. Prosternal ridge well developed, sternite weakly sclerotized. Preoral ridge weakly developed. Ocular sclerite weakly sclerotized near ventral eye. Ventral midcranial ridge well developed, with lateral arms. Ventral eye 39(32–44) μ in diameter.

Antenna 10-segmented with bristle-shaped and fleshy setae, capitate setae present on apical segment; segments I 37(30–40) μ long (Fig. 8H); II 55(49–62) μ long

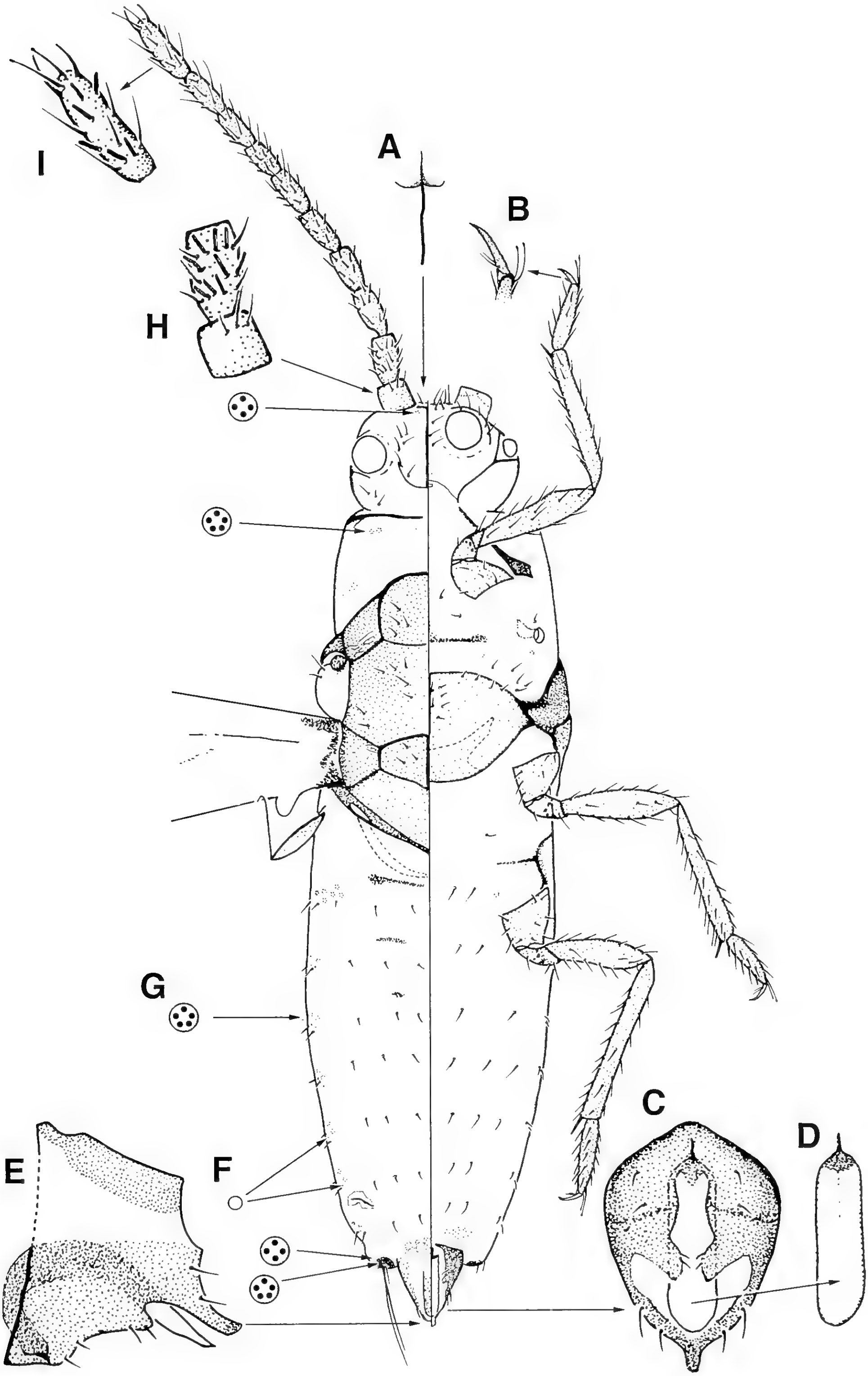

Fig. 8. Adult male of *Paracoccus marginatus.* A, Frontal view of midcranial ridge. B, Detail of front leg. C, Ventral view of penial sheath. D, Aedeagus. E, Lateral view of penial sheath. F, Discoidal pore. G, Quinquelocular pore. H, Detail of scape and pedicel. I, Detail of apical segment.

Table 2. Morphological comparisons of New World *Paracoccus*. Bold indicates characters that differ from *Paraco*[illegible]

Paracoccus Species	Circulus	Number of Cerarii	Oral Rim Distribution	Marginal Cluster Oral Collars Near Anterior Spiracle	Pores on Hind Tibiae
marginatus	yes	16–17	margin only	no	no
alazanensis	yes	17	**margin and abdomen**	no	**yes**
ascius	yes	17	**scattered**	**yes**	**yes**
baccharidicola	yes	**7**	**scattered**	**yes**	**yes**
circuliprivis	**no**	**7**	**margin and thorax**	no	**yes**
decorus	**no**	**7–9**	**throughout except head**	no	**yes**
ferrisi	**variable**	12–17	**usually margin and abdomen**	**yes**	**yes**
hamoni	yes	**12**	**scattered**	no	**yes**
herreni	yes	16	**scattered**	**yes**	**yes**
juniperi	yes	5–17	**scattered**	**yes**	**yes**
lycopersici	yes	**4–7**	**scattered**	**yes**	**yes**
mexicanus	yes	15–17	**scattered**	no	**yes**
myrtacearum	**no**	**14**	**scattered**	no	**yes**
oneratus	yes	**5**	**many, scattered**	no	**yes**
ordinis	yes	15–16	**scattered**	**yes**	**yes**
reductus	yes	**0**	**absent**	no	**yes**
salviacola	yes	16	**scattered**	**yes**	**yes**
solani	**variable**	**6–7**	**scattered**	no	**yes**
townsendi	yes	**13**	**absent**	**yes**	no
turrialbensis	**no**	**7**	**abdomen**	no	**yes**
villanuevai	**yes**	17	**scattered**	**yes**	no

(Fig. 8H); III 68(62–74) μ long; VI 52(45–57) μ long; VII 53(47–59) μ long; VIII 53(47–59) μ long; IX 46(37–49) μ long; X 46(49–69) μ long (Fig. 8I); total length 534(469–563) μ long. Hind femur 145(133–148) μ long; hind tibia 199(163–222) μ long; hind tarsus 83 (69–86) μ long; hind tarsal claw 27(22–32) μ long; hind femur/tibia ratio 0.7; hind tibia/tarsus ratio 2.4(2.3–2.5); leg setae bristle shaped. Tarsal digitules capitate; claw digitules acute (Fig. 8B).

Notes.—The above description is based on 64 specimens from 8 localities. The adult male can be distinguished from all other instars by having a distinct aedeagus, lateral pore clusters, a heavily sclerotized thorax and head, and by having well-developed wings.

Specimens Examined

UNITED STATES: Florida: Broward County, Ft. Lauderdale, on *Hibiscus* sp., 5-XI-1998, by W. Thiel. Manatee County, Bradenton, on *H. rosa-sinensis,* 24-VII-1998, by W. Clifton (2 ad. ♀). Palm Beach County, Boca Raton, on *Hibiscus rosa-sinensis,* 1998, by J. Lofquist (1 ad. ♀). BRITISH VIRGIN ISLANDS: Great Camanoe Island, on *Ipomoea* sp., 16-X-1996, by R. F. Denno (7 ad. ♀). DOMINICAN REPUBLIC: Locality unknown, on *Persea americana,* 19-VII-1994, by J. Sanchez (1 ad. ♀). MEXICO: Baja California—La Paz, on *Carica papaya,* 13-IX-1978, by G. Buxton (16 ad. ♀, 3 third-instar ♀, 3 second-instar ♂). Colima—Cofradia de Juarez, on *Carica papaya,* 8-VI-1999, by H. González, J. Villaneuva, D. R. Miller (1 ad. ♀); Crucero de Perquillos, on *Carica papaya* and *Manihot esculenta,* 8-VI-1999, by H. González, J. Villaneuva, D. R. Miller (3 ad. ♀); Rinxon de Lopez near Ameria, on *Carica papaya,* 8-VI-1999, by H. González, J. Villaneuva, D. R. Miller (1 ad. ♀); near Tecoman, Boca de Pazcuales, on *Carica pa-*

Table 3. Morphological comparisons of selected first instars, second-instar females, third-instar females, and adult females of *Paracoccus marginatus* and other economically important mealybugs. Bold indicates characters that differ from *Paracoccus marginatus*.

	First Instar		Second-Instar Female			Third-Instar Female			Adult Female		
	Anal Bar	# Cerarii	Anal Bar	# Cerarii	Oral Rims	Anal Bar	# Cerarii	Oral Rims	Anal Bar	# Cerarii	Oral Rims
Paracoccus marginatus	yes	7–10	yes	4–11	no	yes	17	no	yes	17	yes
Dysmicoccus brevipes	**no**	**17**	**no**	**17**	no	**no**	17	no	**no**	17	**no**
Ferrisia virgata	**no**	**1**	**no**	**1**	**yes**	**no**	**1**	**yes**	**no**	**1**	yes
Maconellicoccus hirsutus	yes	**1–2**	yes	**3–4**	**yes**	yes	3–4	**yes**	yes	**4–7**	yes
Nipaecoccus nipae	yes	**17**	?	?	?	yes	**10+**	no	**no**	**10+**	**no**
Phenacoccus gossypii/madeirensis	yes	**15–18**	yes	**15–18**	no	yes	**18**	no	yes	**18**	**no**
Phenacoccus solenopis	yes	**15–18**	yes	**15–18**	no	yes	**18**	no	yes	**18**	no
Planococcus citri/minor	yes	**18**	yes	**18**	no	yes	**18**	no	yes	**18**	**rare**
Pseudococcus jackbeardsleyi	**no**	**17**	**no**	**17**	no	**no**	17	**yes**	**no**	17	yes
Pseudococcus longispinus	yes	**17**	yes	**17**	**yes**	yes	17	**yes**	yes	17	yes
Pseudococcus viburni	**no**	**17**	**no**	**17**	no	**no**	17	**yes**	**no**	17	yes

paya, 8-VI-1999, by H. González, J. Villaneuva, D. R. Miller (2 ad. ♀, 1 third-instar ♂); Laguna de Chanchopan, on *Carica papaya,* 10-II-2000, by H. González, J. Villaneuva, M. E. Schauff, D. R. Miller (8 first instar); Puerta de Caberar, on *Carica papaya,* 7-II-2000, by H. González, J. Villaneuva, M. E. Schauff, D. R. Miller (1 ad. ♀, 4 first instar); Plan de Zapotes, on *Carica papaya,* 10-II-2000, H. González, J. Villaneuva, M. E. Schauff, D. R. Miller (4 ad. ♀, 2 ad. ♂, 3 third-instar ♀, 2 second-instar ♂); Colima City, 7-II-2000, on *Carica papaya,* H. González, J. Villaneuva, M. E. Schauff, D. R. Miller (2 ad. ♀, 1 third-instar ♀, 1 second-instar ♀, 1 second-instar ♂). Guerrero—Acapulco Airport, on *Sida* sp., 15-IV-1984, by J. Gillet and H. Miranda (1 ad. ♀); El Carrizal, on *Mimosa pigra,* 7-VII-1986, by J. Gillett (1 ad. ♀). Jalisco—San Marcos, on *Carica papaya,* 6-II-2000, by H. González, J. Villaneuva, M. E. Schauff, D. R. Miller (1 ad. ♀). Michoacan—near Nueva Italia, on *Carica papaya,* 5-II-2000, by H. González, J. Villaneuva, M. E. Schauff, D. R. Miller (2 ad. ♂, 5 third-instar ♀, 4 second-instar ♀); Santa Casilda, on *Carica papaya,* 9-VI-1999, by H. González, J. Villaneuva, D. R. Miller (20 ad. ♀, 3 ad. ♂, 2 third-instar ♀, 1 third-instar ♂, 3 second-instar ♀, 15 first instar). Tobasco—Ejido Lopez Portillo, on *Hibiscus* sp., 4-VI-1999, by H. González, D. R. Miller (1 ad. ♀); Rancherias Barrancar y Amate, on *Carica papaya* and *Manihot esculenta,* 4-VI-1999, H. González, D. R. Miller (2 ad. ♀); Villahermosa, on *Mimosa pigra,* 18-III-1985, by J. Gillet (11 ad. ♀); Villahermosa, on *Hibiscus* sp., 4-VI-1999, by H. González, D. R. Miller (1 ad. ♀). Vera Cruz—Campo Cotaxtla, on *Carica papaya,* 2-VI-1999, by H. González, J. Villaneuva, D. R. Miller (4 ad. ♀); Curva del Pato Santa Fe, on *Hibiscus* sp. and *Manihot esculenta,* 2-VI-1999, by H. González, J. Villaneuva, D. R. Miller (8 ad. ♀); El Mangal, on *Carica papaya,* 2-VI-1999, by H. González, J. Villaneuva, D. R. Miller (7 ad. ♀); Huexotla, on *Carica papaya,* 2-VI-

1999, by H. González, J. Villaneuva, D. R. Miller (1 ad. ♂); Manilo Fabio Altamirano, on *Hibiscus* sp., 2-VI-1999, by H. González, J. Villaneuva, D. R. Miller (5 ad. ♀, 3 third-instar ♀, 1 second-instar ♀); Oaxaquilla, on *Carica papaya,* 2-VI-1999, by H. González, J. Villaneuva, D. R. Miller (33 ad. ♀, 9 third-instar ♀, 9 second-instar ♀, 14 second-instar ♂, 2 first instar); Santa Fe, on *Manihot esculenta,* 2-VI-1999, by H. González, J. Villaneuva, D. R. Miller (5 ad. ♀, 1 third-instar ♀); Tepetates, Colegio de Postgraduados, on Leguminosae, 5-VI-1999, by H. González, J. Villaneuva, D. R. Miller (41 ad. ♀, 4 third-instar ♀, 4 second-instar ♀); Vera Cruz (intercepted at El Paso, Texas), on *Carica papaya,* 25-IV-1983, by R. Venezia (3 ad. ♂). Unknown State—locality unknown (intercepted at Nogales, Arizona), host unknown, 21-VII-1991, by G. Kluzik (2 ad. ♀); locality unknown (intercepted at Nogales, Arizona), host unknown, 5-IX-1991, by T. Giles (1 ad. ♀); locality unknown (intercepted at El Paso, Texas), on *Zea mays,* 20-XI-1992, by H. Grieb (1 ad. ♀). PUERTO RICO: Locality unknown, on *Hibiscus* sp., 24-II-1994, by J. Morales (2 ad. ♀); Locality unknown, on *Carica papaya,* 16-X-1995, by unknown collector (3 ad. ♀). ST. KITTS: Basseterre, CARDI Experimental Farm, on *Carica papaya,* 27 and 26-VII-2000, by G. L. Miller (12 ad. ♀, 1 ad. ♂, 4 third-instar ♀, 11 second-instar ♀, 13 second-instar ♂, 15 first instar). U.S. VIRGIN ISLANDS: St. Croix, on *Plumeria* sp., 16-VIII-1994, by K. Jenkins (1 ad. ♀); St. Thomas—Botany Bay, on *Carica papaya,* 2-VI-1998, by M. E. Schauff and D. R. Miller; near Dorothea Bay, on shrub, 3-VI-1998, by M. E. Schauff and D. R. Miller; John Brew's Bay, on *Acacia* sp., 3-VI-1998, by D. R. Miller; Magens Bay, on *Coccoloba* sp., 4-VI-1998, by M. E. Schauff and D. R. Miller; near Redhook Ferry, Smith Bay, on unknown host, 4-VI-1998, by M. E. Schauff and D. R. Miller; Smith Bay, on leguminose tree, 4-VI-1998, by M. E. Schauff and D. R. Miller; Locality unknown, on *Solanum tuberosum* (in culture), 9-V-2000, by C. Francis (36 ad. ♀, 51 ad. ♂, 8 fourth-instar ♂, 5 third-instar ♀, 14 third-instar ♂, 7 second-instar ♀, 23 second-instar ♂, 41 first instar); Locality unknown, on *Solanum tuberosum* (in culture), 8-VIII-2000, by R. Warkentin (2 ad. ♂, 2 third-instar ♀, 1 third-instar ♂, 24 second-instar ♀, 30 second-instar ♂).

DISCUSSION

A synopsis of selected diagnostic information for slide-mounted adult females of *Paracoccus* occurring in Central and South America is presented in Table 2. Two characters that are important for distinguishing *P. marginatus* from all other species of New World *Paracoccus* are: (1.) presence of oral-rim tubular ducts only on the margin (unique with *P. marginatus*) and (2.) absence of pores on the hind tibiae (only *P. townsendi* and *P. villanuevai* also lack pores on the hind tibiae). In addition, adult females of *P. marginatus* differ from other members of the genus found in Central and South America by having the following combination of characters: a circulus; up to 8 pairs of abdominal cerarii; oral rim tubular ducts present on the dorsal surface; multilocular disk pores absent from ventral lateral margins of thorax; oral rim tubular ducts absent from dorsum of anal lobe; and dorsal oral rim tubular ducts present near margins.

Tables 3–6 also include some diagnostic characters for comparing first instars, second-instar females, third-instar females, and adult females and males to various other mealybugs found on similar hosts to *P. marginatus.* First instars of *P. marginatus* differ from the first instars of many other mealybugs by having an anal bar, a circulus, and 7–10 pairs of indefinite cerarii that are represented by 1 conical seta 1 smaller seta and 1 or 2 associated trilocular pores (see also Table 3). Second-instar *P. marginatus* females differ from the second-instar females of many other mealybugs by having an anal bar, a circulus, and 4–11 pairs of indefinite cerarii (see also Table 3). Sec-

Table 4. Morphological comparisons of second-instar males of *Paracoccus marginatus* and other economically important mealybugs. Bold indicates characters that differ from *Paracoccus marginatus*.

	Second-Instar Male				
	Multilocular Pores	Anal-lobe Bar	# Cerarii	Discoidal Pore Near Eye	Oral Rim Tubular Ducts
Paracoccus marginatus	present	present	10+ pair	absent	absent
Dysmicoccus brevipes	**absent**	**absent**	17 pair	**present**	absent
Ferrisia virgata	**absent**	**absent**	**1 pair**	absent	absent
Maconellicoccus hirsutus	**absent**	present	**1 or 2 pair**	absent	usually absent
Nipaecoccus nipae	present	present?	10+ pair	**present**	**present**
Phenacoccus gossypii/madeirensis	**absent**	present	15–18	absent	absent
Phenacoccus solenopis	**absent**	present	15–18	absent	absent
Planococcus citri/minor	present	present	10+ pair	absent	absent
Pseudococcus jackbeardsleyi	**absent**	**absent**	17 pair	**present**	absent
Pseudococcus longispinus	**absent**	present	17 pair	absent	absent
Pseudococcus viburni	**absent**	**absent**	17 pair	**present**	absent

ond-instar males of *P. marginatus* differ from the second-instar males of many other mealybugs by having multilocular disk pores on dorsum and venter of thorax, an anal bar, a circulus, 10 or more pairs of indefinite cerarii, and numerous dorsal oral-collar tubular ducts (see also Table 4). *Paracoccus marginatus* third-instar females differ from the third-instar females of many other mealybugs by lacking oral-collar and oral-rim tubular ducts and multilocular pores; and by having an anal bar, circulus, and 17 pairs of indefinite cerarii (see also Table 3).

In comparison with the species listed in Table 5, adult males of *P. marginatus* are different from the other species listed by the following two characters: (1.) presence of stout fleshy setae on the antennae and (2.) absence of fleshy setae on the legs. *Paracoccus marginatus* adult males are most similar to *Planococcus citri* (Risso) but, in addition to the aforementioned characters, *P. marginatus* differs by having margins of abdominal segments I with 5(3–7) multilocular pores in each lateral cluster, usually without multilocular pores on head, and a broad aedeagus. *Planococcus citri* has long fleshy setae on the antennae, many fleshy setae on the legs, margins of abdominal segments I with 14(11–18) multilocular pores in each lateral cluster, usually with 2 multilocular pores on head, narrow aedeagus.

Although examination of microscope slide-mounted material is imperative for proper species determination, field characters are sometimes useful for preliminary identification. Table 6 includes a comparison between *P. marginatus* and common mealybugs based on the number of lateral filaments, caudal filament length as compared to body length, body color, dorsal body stripes, and position of the ovisac. A category for other unique characters is also included. *Paracoccus marginatus* can be distinguished readily from the other included species by caudal filament length, body color, and position of the ovisac.

Invasive scale insect pests are responsible for millions of dollars in crop loss in the United States. *Paracoccus marginatus* represents yet another scale insect that has drawn attention as an invasive species. It, other scale pests, and potential scale pests have recently been identified because of their threat to U.S. agriculture (Miller and Miller, in press). A critical element in any program that involves control or management of an insect pest should always first begin with the correct identification. This paper contributes toward this end. We found that all stages of *P. marginatus* can be separated intraspecifically. In addition,

Table 5. Morphological comparisons of adult males of *Paracoccus marginatus* and other economically important mealybugs. Bold indicates characters that differ from *Paracoccus marginatus*.

	Adult Male (Fifth Instar)						
	Fleshy Setae on Legs	Fleshy Setae on Abdomen	Fleshy Setae on Antennae	Lateral Clusters of Pores on Abdomen	Tail-forming Pore Clusters	Setae on 8 Abdominal Terga	[illegible]
Paracoccus marginatus	no	no	short	small, all segments	1 pair	rarely	[illegible]
Dysmicoccus brevipes	**yes**	**yes**	**long**	small, all segments	1 pair	**yes**	absent
Ferrisia virgata	**yes**	**yes**	**long**	small, all segments	1 pair	**yes**	absent
Maconellicoccus hirsutus	**yes**	no	**long**	**small, anterior segments**	1 pair	**yes**	absent
Nipaecoccus nipae	**yes**	no	**long**	**large, all segments**	1 pair	**yes**	small
Phenacoccus gossypii/madeirensis	**yes**	no	**long**	small, all segments	**2 pair**	**yes**	**absent**
Phenacoccus solenopis	**yes**	no	**long**	small, 0–3 on all segments	**2 pair**	**yes**	**absent**
Planococcus citri/minor	**yes**	no	**long**	**large, all segments**	1 pair	**yes**	small
Pseudococcus jackbeardsleyi	**yes**	**yes**	**long**	**large, all segments**	1 pair	**yes**	**absent**
Pseudococcus longispinus	**yes**	**yes**	**long**	small, all segments	1 pair	**yes**	**large**
Pseudococcus viburni	**yes**	**yes**	**long**	**large, all segments**	1 pair	**yes**	**absent**

Table 6. Field character comparisons of adult females of *Paracoccus marginatus* and other economically important mealybugs. Bold indicates characters that differ from *Paracoccus marginatus*.

	Field Characters of Adult Females					
	# Lateral Filaments	Caudal Filament Length to Body Length	Body Color	Dorsal Body Stripes	Position of Ovisac	Other Unique Characters
Paracoccus marginatus	many	about ¼	**greenish yellow**	no	beneath and behind body	
Dysmicoccus brevipes	many	¼ to ½	**pink**	no	**no**	
Ferrisia virgata	**1 pair**	¼ to ½	grayish	**2**	**no**	**crystalline rods on dorsum**
Maconellicoccus hirsutus	**absent, rarely 1 or 2**	short	**reddish brown**	no	beneath body	
Nipaecoccus nipae	many	about ¼	**red**	no	**no**	**filaments on dorsum**
Phenacoccus gossypii/madeirensis	many	less than ¼	gray	**2**	**covers body**	
Phenacoccus solenopis	many	less than ¼	green	**2**	**no**	large body
Planococcus citri/minor	many	less than ¼	**pink**	**1**	beneath body	
Pseudococcus jackbeardsleyi	many	**about ½**	**pink?**	no	**covers part of body**	**filaments thin**
Pseudococcus longispinus	many	**as long as body**	gray	**1**	**no**	**hind 2 pair of filaments long**
Pseudococcus viburni	many	**about ½**	**pink**	no	**covers part of body?**	**filaments thin**

we have listed various synoptic characters which are diagnostic when compared with many of the common pests that occur on similar hosts of *P. marginatus.*

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CHILACIS TYPHAE (PERRIN) AND *HOLCOCRANUM SATUREJAE* (KOLENATI) (HEMIPTERA: LYGAEOIDEA: ARTHENEIDAE): UPDATED NORTH AMERICAN DISTRIBUTIONS OF TWO PALEARCTIC CATTAIL BUGS

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Abstract.—*Chilacis typhae* and *Holcocranum saturejae,* Palearctic lygaeoids that feed on cattail seeds, were first reported from North America in 1987 and 1995, respectively. Additional fieldwork provided 21 new state records for *C. typhae* and 15 for *H. saturejae,* plus the first records from the Canadian Maritime Provinces for *C. typhae,* which has a more northern distribution than *H. saturejae.* The bugs were syntopic—that is, occurred in the same cattail colonies—in Delaware, Illinois, Indiana, Kentucky, Maryland, Missouri, Ohio, Pennsylvania, Tennessee, Virginia, and West Virginia. In addition, 25 of the 50 sites from which *C. typhae* was originally collected (1986) in Delaware, Maryland, New York, and Pennsylvania were resampled in 1998. *Holcocranum saturejae,* collected at only two sites in 1986 (but not recognized until 1995), was present in 1998 at nine of the original sites in Delaware, Maryland, and southern Pennsylvania; as in 1986, this species was not found in New York or in more northern sites in Pennsylvania.

Key Words: Insect distribution, adventive species, Heteroptera, *Typha*

When the Old World cattail bug *Chilacis typhae* (Perrin) was reported new to North America (Wheeler and Fetter 1987), it also represented the first Nearctic record of the lygaeid subfamily Artheneinae. The paper by Wheeler and Fetter (1987) seemed straightforward, documenting the establishment of another Palearctic insect in the northeastern United States. But instead of a single immigrant cattail lygaeid of presumed northeastern distribution, the North American fauna, in at least some of the more southern sites for *C. typhae,* actually contained two widely distributed Old World cattail bugs. Since the appearance of Wheeler and Fetter's (1987) paper, a second Old World artheneine, *Holcocranum saturejae* (Kolenati), of similar habitus and seed-feeding habits on cattail, was reported from the eastern United States (Hoffman and Slater 1995). At two of the 50 localities (New Castle Co., Del.; Chester Co., Pa.) from which *C. typhae* originally was reported, a reexamination of voucher material revealed a few adults of *H. saturejae* that had been overlooked among adults of *C. typhae* (Hoffman 1996, Wheeler and Stoops 1999). Both cattail bugs now have been recorded from the western United States: *C. typhae* in the Pacific Northwest and *H. saturejae* from California to Texas (Wheeler and Stoops 1999). *Chilacis typhae* also is known in Canada from British Columbia and Ontario (Maw et al. 2000). *Holcocranum saturejae* shows a more southern distribution than *C. typhae* in the Old and New Worlds (Hoffman and Slater 1995, Hoffman 1996, Wheeler and Stoops 1999). In addition, the Artheneinae have recently been accorded family status—Artheneidae—in the Lygaeoidea (Henry 1997).

Holcocranum saturejae has become established in areas of the eastern United States where only *C. typhae* was collected in 1986. To obtain distributional data that might help subsequent workers assess changes in the ranges of these adventive species, I conducted additional surveys, emphasizing areas of the bugs' syntopy. I also hypothesized, based on the apparent rapid dispersal ability of *H. saturejae* (Hoffman 1996), that more of the cattail colonies initially sampled for *C. typhae* in 1986 would yield *H. saturejae* rather than only the one site each in Delaware and Pennsylvania.

METHODS

Because extensive systematic sampling of cattails in Canada and the United States was not feasible, cattail colonies (mainly *T. angustifolia* L. and *T. latifolia* L.) were selected haphazardly from a more limited area of North America. Areas where the two artheneids potentially co-occur were sampled more intensively. Voucher specimens have been deposited in the Cornell University Insect Collection, Ithaca, N.Y., and the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

In 1998, I resampled 25 of the 50 cattail sites from which *C. typhae* was originally collected (Wheeler and Fetter 1987) to determine if *H. saturejae* was present at the 23 sites that previously yielded only *C. typhae*, and whether *H. saturejae* might now be the more common artheneid at the two sites where both species were collected in 1986. When the same cattail stands sampled in 1986 could not be located (n = 1), no longer existed (n = 1), or did not contain old pistillate spikes or heads (n = 2), a colony within 1–2 km was substituted. In the field, old cattail heads were pulled apart over a white enamel pan and the numbers of adults of both artheneid species were recorded. All pistillate heads from the previous season were sampled when five or fewer were accessible; as many as 10 heads were examined in cattail colonies with numerous heads available.

DISTRIBUTION

In the following list of additional records for *C. typhae* and *H. saturejae* (see also Figs. 1–2), new state and provincial records are indicated by asterisks. Canadian records of *C. typhae* were obtained during fieldwork with E. R. Hoebeke; Florida records of *H. saturejae* in 1997, during fieldwork with C. A. Stoops; and the records of *C. typhae* from Nebraska in August 1998 and the Kansas record and 1999 Oklahoma records of *H. saturejae*, during fieldwork with T. J. Henry. Unless otherwise stated, all other collections were made by the author. Table 1 gives the numbers of *C. typhae* and *H. saturejae* adults observed in 1998 in cattail heads at 25 of the 50 sites at which *C. typhae* was detected in 1986.

Chilacis typhae.—CANADA: *NEW BRUNSWICK: York Co., Fredericton, 27 June 1993. *NOVA SCOTIA: Antigonish Co., Rt. 104, Beaver Meadow Rd./James River Exit, 22 July 1995; Colchester Co., Truro, 22 July 1995; Lunenburg Co., Rt. 3 nr. Mader's Cove (SE of Mahone Bay, NW of Lunenburg), 21 July 1995; Pictou Co., Rt. 104, Thorburn exit, 22 July 1995; Victoria Co., Cape Breton Island, Baddeck, 25 July 1995. *PRINCE EDWARD ISLAND: Kings Co., jct. rts. 4 & 315, SE of Montague, 25 July 1995; Prince Co., Summerside, 26 July 1995; Queens Co., Cavendish, 26 July 1995. UNITED STATES: *CONNECTICUT: Fairfield Co., Rt. 39 S of Rt. 55, SW of Gaylordsville, 13 Aug. 2000; Litchfield Co., Rt. 8, Torrington, 12 Aug. 2000; New Haven Co., Rt. 64, Middlebury, 13 Aug. 2000. *ILLINOIS: Iroquois Co., Rt. 24, Watseka, 2 July 2000; Jackson Co., Rt. 13, Carbondale & Rt. 51, 2 km N of Carbondale, 21 June 1998; La Salle Co., rts. 39 & 51 N of jct. Rt. 80, ca. 5 km NE of LaSalle, 2 July 2000; Lee Co., rts. 39 & 51 exit 82, W of Paw Paw, 2 July 2000; Liv-

Table 1. Numbers of *C. typhae* and *H. saturejae* in cattail heads, 26–30 July 1998, at sites from which *C. typhae* [illegible] to North America in 1986. Names of localities follow those of Wheeler and Fetter (1987); asterisks indicate the two sites positive for *H. saturejae* in 1986.

Collection Sites	*C. typhae*	*H. saturejae*
DELAWARE		
New Castle Co., E of Newark	7	272
MARYLAND		
Frederick Co., Emmitsburg	72	7
NEW YORK		
Broome Co., nr. Castle Creek	71	0
Broome Co., S of Kirkwood	39	0
Tompkins Co., Besemer	229	0
Tompkins Co., S of Ithaca	59	0
PENNSYLVANIA		
Adams Co., S of East Berlin	2	0
Adams Co., nr. Gettysburg	53	4
Berks Co., nr. Frystown	34	17
Berks Co., nr. Hamburg	77	0
Berks Co., nr. Rehrersburg	7	0
*Chester Co., Longwood Gardens	25	73
Cumberland Co., nr. Wertzville	10	14
Dauphin Co., nr. Harrisburg Area Community College	2	126
Lackawanna Co., E of Factoryville	18	0
Lebanon Co., W of Licksdale	110	0
Monroe Co., Sciota	46	0
Schuylkill Co., Barnesville	23	0
Schuylkill Co., nr. Ravine	248	0
Susquehanna Co., Great Bend	125	0
Wayne Co., Beach Lake	72	0
Wayne Co., S of Hoadleys	123	0
Wyoming Co., E of Dixon	59	0
York Co., S of Dillsburg	300	5
York Co., SW of Kralltown	1	4

ingston Co., Rt. 24, 7.5 km E of Forrest, 2 July 2000; Marion Co., Rt. 51, 1.5 km N of Central City & Rt. 51, S of Centralia nr. Washington Co. line, 21 June 1998; Ogle Co., rts. 39 & 51 exit 111, W of Monroe, 2 July 2000; Pike Co., rts. 36 & 72, 8 km W of Barry, 20 June 1998; Sangamon Co., jct. Rt. 72 & Rt. 4, Springfield, 20 June 1998. *INDIANA: Elkhart Co., jct. rts. 19 & 20, S of Elkhart, 2 July 2000; Floyd Co., Rt. 265, New Albany, 8 July 1997; Gibson Co. Rt. 64, Oakland City, 24 June 2000; LaPorte Co., Rt. 30, 6 km E of Wanatah, 2 July 2000; Marshall Co., Rt. 30, Plymouth, 2 July 2000; Newton Co., Rt. 24, 7.5 km E of Kentland, 2 July 2000; Pulaski Co., Rt. 421, 1.5 km N of Medaryville, 2 July 2000; St. Joseph Co., Pleasant Lake, Lakeville, 2 July 2000; Starke Co., Rt. 30, 2.5 km E of Hamlet, 2 July 2000; White Co., Rt. 421, 2.5 km S of Monon, 2 July 2000. *IOWA: Allamakee Co., Waukon, 3 July 2000; Clayton Co., Rt. 18, Marquette, 3 July 2000. *KENTUCKY: Bullitt Co., Rt. 65, W of Clermont, 9 July 1997 & Rt. 65, 0.5 km S of exit 112, 3.2 km SW of Clermont, 25 June 2000; Carroll Co., Rt. 227 nr. jct. Rt. 71, 8 July 1997; Metcalfe Co., Cumberland Parkway, 12.5 km NE of Edmonton, 3 July 1999; Oldham Co., Rt. 42, S of Skylight, 8 July 1997; Pike Co., Rt. 23, 4 km S of Pikeville, 29 June 2000. *MAINE: Sagadahoc

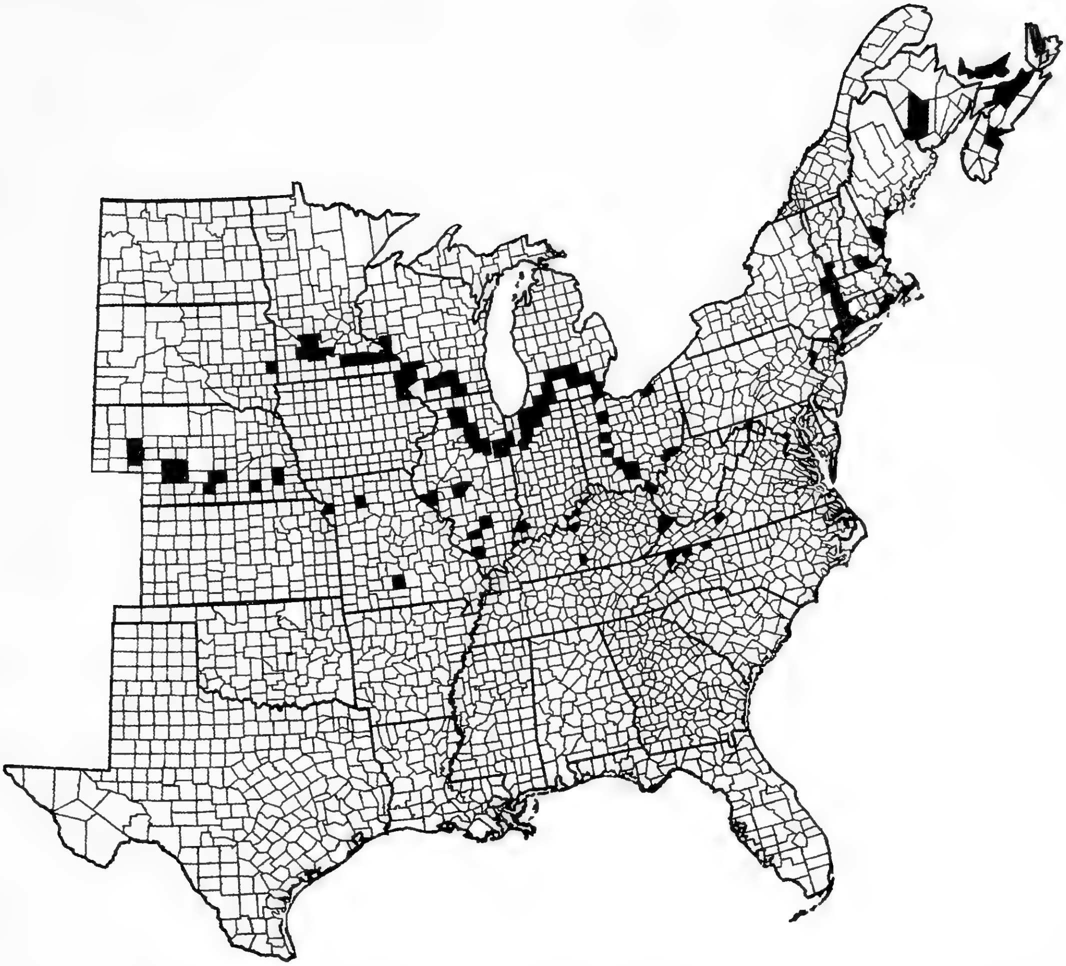

Fig. 1. New eastern North American records for *Chilacis typhae*. Previous eastern U.S. records are not shown but are available in publications by Wheeler and Fetter (1987), Hoffman and Slater (1995), and Hoffman (1996); western U.S. records were given by Wheeler and Stoops (1999).

Co., Rt. 1, Woolrich, 23 June 1993, E.R. Hoebeke and AGW; York Co., Appledore Island, Isles of Shoals, 11 Aug. 2000, W. Reeves; Kittery, 22 July 2000, E.R. Hoebeke; Rt. 1, Moody, 29 June 1989. *MASSACHUSETTS: Barnstable Co., Rt. 6A, West Brewster, 28 May 1989; Berkshire Co., Rt. 8, North Adams & Pittsfield, 12 Aug. 2000; Suffolk Co., Arnold Arboretum, Jamaica Plains, 27 May 1988, E. R. Hoebeke and AGW. *MICHIGAN: Barry Co., jct. rts. 37 & 79, 4 km SE of Hastings, 1 July 2000; Cass Co., Rt. 40, 5 km S of Jones, 1 July 2000; Eaton Co., Rt. 50, 5.5 km E of Charlotte, 1 July 2000; Ingham Co., Holt, 1 July 2000; Jackson Co., Austin Rd., 3.5 km E of Napoleon, 1 July 2000; Kalamazoo Co., bus. rts. 94 & 131, Kalamazoo, 1 July 2000; Monroe Co., Rt. 50, E of Dundee & Rt. 75, W of Newport, 1 July 2000; St. Joseph Co., Rt. 60, 3 km SW of Three Rivers, 1 July 2000; Washtenaw Co., Rt. 12, Saline, 1 July 2000. *MINNESOTA: Brown Co., Rt. 14, Essig, 4 July 2000; Dodge Co., Rt. 14, 1 km W of Dodge, 3 July 2000; Nicollet Co., Rt. 14, North Mankato, 4 July 2000; Olmsted Co., Co. Rd. 10, S of Dover, 3 July 2000; Redwood Co., Rt.

14, Redwood Falls, 4 July 2000; Renville Co., Rt. 212, 2 km W of Sacred Heart, 4 July 2000; Steele Co., Rt. 14, 8 km E of Owatonna, 3 July 2000; Waseka Co., Clear Lake, Waseka, 4 July 2000; Winona Co., Winona, 3 July 2000. *MISSOURI: Buchanan Co., Rt. 36, W of Rt. 31, NW of Easton, 20 June 1998; Livingston Co., Rt. 36, E of Chillicothe, 20 June 1998; Wright Co., Hillcrest Cemetery, Mountain Grove, 8 July 2000. *NEBRASKA: Buffalo Co., Rt. 80, 5.5 km W of Kearney, 18 Aug. 1998; Fillmore Co., Rt. 36, 5.5 km W of Exeter, 21 Aug. 1998; Garden Co., Rt. 26, 3.5 km SE of Lewellen, 16 June 1998; Lancaster Co., Rt. 77, 4.5 km S of Ceresco, 17 Aug. 1998 & 12.5 km S of Lincoln, 16 Aug. 1998; Lincoln Co., Rt. 83, 9 km N of North Platte, 13 June 1998; Phelps Co., 5.5 km N of Funk, 21 Aug. 1998. *NEW HAMPSHIRE: Hillsborough Co., Petersborough, 6 Aug. 1995. *NEW JERSEY: Warren Co., Rt. 521, Hope, 29 July 1998. NEW YORK: Putnam Co., Rt. 22, SE of Patterson, 13 Aug. 2000; Rensselaer Co., Rt. 2, Grafton, 12 Aug. 2000. *NORTH CAROLINA: Alleghany Co., Rt. 21, Cherry Lane (16 km S of Sparta), 27 July 2000. *OHIO: Clark Co., Rt. 72, 8.5 km S of Springfield, 30 June 2000; Cuyahoga Co., Brook Park, 8 Aug. 1992; Erie Co., Huron, 8 Aug. 1992, E. R. Hoebeke; Fayette Co., Rt. 35, 4 km SW of Washington Court House, 30 June 2000; Hancock Co., Rt. 68, 1.3 km S of Williamstown, 30 June 2000; Lawrence Co., Rt. 93 nr. jct. Rt. 52, Ironton, 30 June 2000; Logan Co., Rt. 68, 4 km S of Bellefontaine, 30 June 2000; Lucas Co., 3 km W of Rt. 75, Toledo, 1 July 2000; Pike Co., Rt. 52, Piketon, 30 June 2000; Ross Co., Rt. 35 nr. jct. Co. Rd. 550, NW of Pleasant Valley, 30 June 2000; Washington Co., Marietta, 30 Apr. 1999; Wood Co., Rt. 75, W of Cygnet, 30 June 2000. *RHODE ISLAND: Washington Co., Rt. 138 E of jct. Rt. 112, W of West Kingston, 29 May 1988 (nymphs only). *SOUTH DAKOTA: Moody Co., Rt. 29 exit 114, W of Flandreau, 4 July 2000. TENNESSEE: Johnson Co., Rt. 91, 0.4 km S of Laurel Bloomery & Rt. 421, Mountain City, 11 July 1999; Sullivan Co., Rt. 11W, 10 km W of jct. Rt. 37, ca. 1 km W of Arcadia, 11 July 1999; Washington Co., Rt. 321, 0.7 km E of jct. rts. 23 & 181, Johnson City, 10 July 1999. *VERMONT: Bennington Co., Rt. 9, 5.5 km W of Bennington, 6 Aug. 1995. *VIRGINIA: Montgomery Co., Rt. 460, 0.5 km N of Rt. 114, Christiansburg, 15 Aug. 2000. *WEST VIRGINIA: Morgan Co., Rt. 9, 1.35 km W of Holton, 28 July 2000. *WISCONSIN: Buffalo Co., Rt. 54, 2.7 km E of jct. Co. Rd. M, SE of Fountain City, 3 July 2000; Crawford Co., Rt. 35, DeSoto, 3 July 2000; Dane Co., Rt. 18 exit Co. Rd. PB, W of Fitchburg, 3 July 2000; Iowa Co., Rt. 18, Cobb, 3 July 2000; Rock Co., rts. 39 & 90, Janesville, 3 July 2000; Vernon Co., Rt. 35, Genoa, 3 July 2000.

Holcocranum saturejae.—UNITED STATES: *ALABAMA: Barbour Co., Rt. 431, 5.5 km N of Eufaula, 9 Apr. 1997 & Rt. 82, 3.5 km NW of Comer, 23 Oct. 1998; Cherokee Co., nr. Centre, 10 Jan. 1999, W. Reeves; Covington Co., Florala, 28 Feb. 1999; DeKalb Co., Rt. 117, 3 km NW of Ider, 3 May 2000; Jackson Co., Rt. 72, 1.5 km E of Hollywood, 5 July 1999; Russell Co., Rt. 431, Seale, 9 Apr. 1997. *ARKANSAS: Ashley Co., Rt. 82, W of Crossett, 21 Apr. 2000; Clay Co., Rt. 62, Corning, 8 July 2000; Columbia Co., Rt. 82, Magnolia, 22 Apr. 2000; Lafayette Co., Rt. 82, Stamps, 22 Apr. 2000; Lawrence Co., rts. 62 & 412, Ravenden, 8 July 2000; Sevier Co., De Queen, 22 Apr. 2000; Union Co., Rt. 82, Strong, 22 Apr. 2000. FLORIDA: Alachua Co., Orange Heights, 20 Mar. 1997; Bay Co., Panama City Beach, 18 Mar. 1997; Hamilton Co., Rt. 6, Jasper, 16 Sept. 2000; St. Johns Co., Anastasia Island State Recreation Area, SE of St. Augustine, 20 Mar. 1997. *GEORGIA: Dade Co., jct. rts. 24 & 299, 1.7 km NNW of Wildwood, 5 July 1999; McDuffie Co., Rt. 78, 2 km SE of Thomson, 17 June 2000. *ILLINOIS: Jackson Co., Rt. 13, Carbondale, 21 June 1998; Massac Co., Rt. 45, N of Grinnell, 21

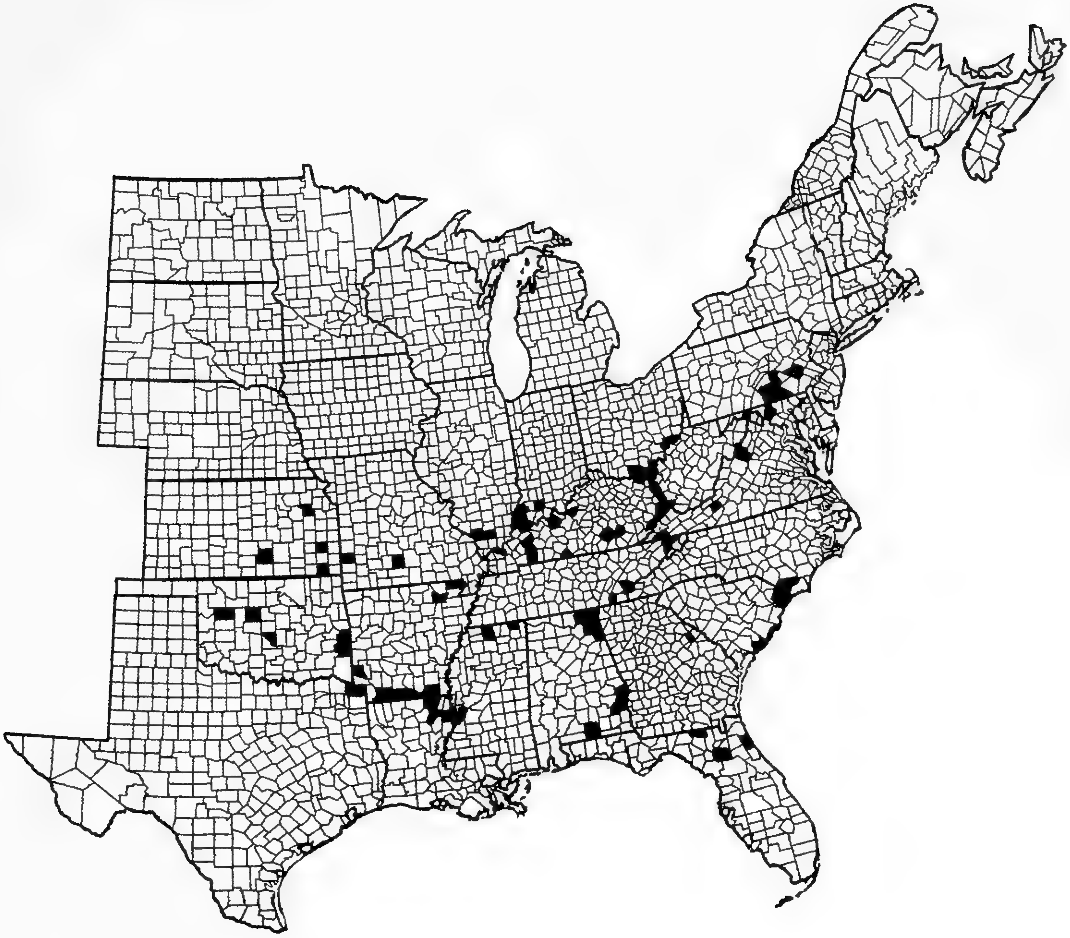

Fig. 2. New eastern U.S. records for *Holcocranum saturejae*. Previous eastern U.S. records are not shown but are available in publications by Hoffman and Slater (1995) and Hoffman (1996); new western U.S. records were given by Wheeler and Stoops (1999).

June 1998; Williamson Co., 3.5 km W of Marion, 7 June 1998. *INDIANA: Dubois Co., Rt. 64, Huntingburg, 24 June 2000; Gibson Co., Rt. 64, Oakland City & Rt. 64, 5 km E of Princeton, 24 June 2000; Posey Co., Rt. 69, 4 km SE of Farmersville & Rt. 165, 4 km S of Poseyville, 24 June 2000; Vanderburgh Co., University of Southern Indiana, W of Evansville, 24 June 2000. *KANSAS: Allen Co., Rt. 169 S of jct. Co. Rd. 224, E of Petrolia, 7 July 2000; Labette Co., Rt. 400, 8 km W of Parsons, 7 July 2000; Sedgwick Co., 53rd St. nr. Rt. 135, ca. 2 km S of Park City, 21 June 1999; Shawnee Co., Rt. 75 S of Rt. 470, Topeka, 7 July 2000. *KENTUCKY: Allen Co., rts. 31E & 231, 7.4 km N of Tennessee state line, NNE of Adolphus, 4 July 1999; Breckinridge Co., Rt. 60, 2 km W of Cloverport, 24 June 2000; Bullitt Co., Rt. 65, 0.5 km S of exit 112, 3.2 km SW of Clermont, 25 June 2000; Christian Co., Pennyrile Parkway, 11 km S of Crofton, 23 June 2000; Greenup Co., Rt. 23, 8 km N of Greenup, 2 May 1999; Henderson Co., Pennyrile Parkway, 0.5 km S of exit 76, S of Henderson, 23 June 2000; Hopkins Co., Pennyrile Parkway, Madisonville, 23 June 2000; Laurel Co., Rt. 80, 3 km W of London, 25 June 2000; Letcher Co., Rt. 23, NE of Jenkins, 29 June 2000; Pike Co., Rt. 23, 4 km S of Pikeville, 29 June 2000; Pulaski Co., Rt. 80, 5 km SW of jct. Rt. 461, 9 km NE of Somerset, 25 June 2000. *LOUISIANA: Madison Par., Rt. 80, 8.6 km E of Waverly, 21 Apr. 2000; Morehouse Par., Rt. 165, 2 km S of Bastrop, 21 Apr. 2000; Richland Par., Rest Area Rt. 20 (west bound), 5 km W of Delhi, 21 Apr. 2000. *MARYLAND: See Table 1. *MISSISSIPPI: Alcorn Co., Rt. 2, 1.5 km SW of Corinth, 5 July 1999; Marshall Co., Rt. 78, 2 km NW of Holly Springs, 5 July 1999; Warren Co., Rt. 27, 1.3 km SE of Rt. 80, SE of Vicksburg, 20 Apr. 2000. *MISSOURI: Barton Co., Rt. 160, 1.5 km W of Mindenmines, 7 July 2000; Wright Co., Hillcrest Cemetery, Mountain Grove, 8 July 2000. NORTH CAROLINA: Columbus Co., Whiteville, 4 Nov. 2000. *OHIO: Gallia Co., Kanauga, 1 May 1999; Lawrence Co., Rt. 93 nr jct. Rt. 52, Ironton, 30 June 2000; Scioto Co., Rt. 52, NE of Franklin Furnace, 30 June 2000; Washington Co., Marietta, 30 Apr. 1999. *OKLAHOMA: Cleveland Co., University of Oklahoma, Norman, 12 June 1999; Dewey Co., Rt. 60, 2 km W of Seiling, 26 Apr. 2000; Kingfisher Co., Rt. 81, 1.1 km S of Dover, 25 Apr. 2000; LeFlore Co., Rt. 59, Howe, 16 June 1999. PENNSYLVANIA: See Table 1. SOUTH CAROLINA: Charleston Co., James Island County Park, 2 May 1998; Horry Co., Longs, 3 Nov. 2000. *TENNESSEE: Bradley Co., Rt. 75, N of McDonald, 24 June 2000; Monroe Co., Rt. 68, 3.5 km S of Tellico Plains, 7 July 1997; Sullivan Co., Rt. 11W, 10 km W of jct. Rt. 37, ca. 1 km W of Arcadia, 11 July 1999; Washington Co., Rt. 321, 0.7 km E of jct. rts. 23 & 181, Johnson City, 10 July 1999. TEXAS: Bowie Co., Rt. 82, 3 km W of New Boston, 2 May 2000. VIRGINIA: Montgomery Co., Rt. 460, 0.5 km N of Rt. 114, Christiansburg, 15 Aug. 2000; Rockingham Co., New Market, 1 Aug. 1998; Scott Co., Rt. 23, Duffield, 29 June 2000. *WEST VIRGINIA: Mingo Co., Rt. 52, 5 km SE of Naugatuck, 29 June 2000; Morgan Co., Rt. 9, 1.35 km W of Holton, 28 July 2000; Wayne Co., Rt. 52, Crum & Rt. 52, 3 km SE of Fort Gay, 29 June 2000.

Discussion

When the Old World cattail bugs *C. typhae* and *H. saturejae* were first reported from the New World, they were assumed to be adventive and to occur only in the eastern United States. Arguments against a Holarctic status for both species were summarized by Wheeler and Stoops (1999). About 15 years after their detection, both species show essentially a transcontinental distribution in the United States and continue to expand their ranges. In addition, *C. typhae* is established in western and eastern Canada. The collection of the more southern *H. saturejae* in southern Arizona and southern Texas suggests its presence in nearby areas of northern Mexico.

Both cattail bugs also have been assumed to represent relatively recent additions to the North American fauna. Claassen's (1921) detailed study of the insects associated with cattails in the Ithaca, N.Y., area during 1916 and 1918 provides historical data on the northeastern cattail fauna. Had *C. typhae* been established at Ithaca in the early 1900s, Claassen likely would have collected it; he observed a native seed-feeding lygaeid, *Kleidocerys resedae* (Panzer), in cattail heads. *Chilacis typhae,* however, could have been established in the Northeast but not present in the cattail colonies Claassen (1921) studied. His paper cannot be considered a baseline study for *H. saturejae,* which is not known as far north as New York. Cattails received little attention from entomologists in the 65 years between the publication of Claassen's (1921) study and the discovery of *C. typhae* in 1986. A study of insect herbivory in Minnesota cattail stands excluded inflorescence feeders (Penko and Pratt 1987). No North American specimens of either species predating the collections of Wheeler and Fetter (1987) or Hoffman and Slater (1995) are known. In addition, neither of the cattail bugs is likely to be collected from plants other than *Typha* species (Hoffman and Slater 1995, Hoffman 1996; A. G. W., personal observation). Thus, the presence of these cattail bugs in North America might have been overlooked for many years.

Hoffman (1996) noted the "intriguing entomological mystery" of the bugs' large populations yet recent detection in North America. Whether these lygaeoids might have been accidentally introduced with cattail heads, the "fluff" of which has been used for insulation and as stuffing for cushions, mattresses, pillows, and toys (Morton 1975, Thieret and Luken 1996), is unknown. Also not known is whether separate introductions to the east and west coasts were involved. How these bugs locate small, sometimes remote host patches and rapidly (<5 years) develop large densities in disturbed or newly created wetlands (Hoffman 1996) also is unanswered. Interstate and other highways, with their associated cattail stands, might serve as corridors that facilitate colonization of new host patches.

My resampling in 1998 of 25 of the original detection sites for *C. typhae* in Delaware, Maryland, and eastern Pennsylvania suggests that since 1986 *H. saturejae* has colonized and become the dominant artheneid at three of those sites. The latter species also was found during 2000 in a cattail colony in Bullitt County, Ky., from which it was not collected in 1997. As *H. saturejae* expands its range northward, it might replace *C. typhae* in some cattail colonies. *Kleidocerys resedae,* unlike the two adventive cattail bugs, is a generalist seed feeder. If displaced on cattails by *C. typhae* or *H. saturejae, K. resedae* could maintain populations on other hosts, especially birches and ericaceous plants (Wheeler 1976).

Syntopic populations of *C. typhae* and *H. saturejae* were observed in 11 states. Between the latitudes of 36°2′ and 40°3′N, these lygaeoids not only were collected from the same cattail colonies, but mixed populations of these species also were found in the same pistillate spikes. The southernmost populations of *C. typhae* tend to be found at higher elevations, for example, in North Carolina at about 870 m and about 505 m at Johnson City, Tenn.

Changes in the ranges and densities of *C. typhae* and *H. saturejae* should continue to be monitored. Distributional data are lacking for much of western North America, especially in Canada between British Columbia and Ontario, and in the United States for Colorado, Idaho, Montana, North Dakota, Utah, and Wyoming. The interactions among the two adventive seed bugs and the native *K. resedae,* as well as the potential effects of *C. typhae* and *H. saturejae* on the arthropod community of cattail heads, offer opportunities for ecological research in the field and laboratory.

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REPRODUCTIVE AND ELECTROPHORETIC COMPARISONS OF *TRICHOGRAMMA CALIFORNICUM* NAGARAJA AND NAGARKATTI WITH THE *T. MINUTUM* COMPLEX (HYMENOPTERA: TRICHOGRAMMATIDAE)

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Abstract.—*Trichogramma californicum* Nagaraja and Nagarkatti was compared with the *T. minutum* Riley complex, with which it is syntopic on codling moth and other tortricid pests. Reproductive crosses and allozymic electrophoresis at 14 loci were used to investigate the possibility of intermediates between them being due to interbreeding. A high degree of intraspecific variation was found for *T. californicum* in both investigations. No reproductive compatibility with *T. minutum* complex cultures was found, and three putatively distinct loci for *T. californicum* were discovered. The implications of these findings for the definition of *T. californicum* are discussed with reference to previous studies of the *T. minutum* complex.

Key Words: *Trichogramma,* taxonomy, interspecific comparisons

Trichogramma is the most important genus of egg parasitoids of Tortricidae in tree crops (Mills and Carl 1991), and is routinely released in augmentative biological control programs, although with mixed success (Falcon and Huber 1991, Smith 1996). By far the most commonly used species in augmentative control efforts of these pests in North America are the two species of the *T. minutum* complex, *T. minutum* Riley and *T. platneri* Nagarkatti. They are allopatric, with *T. minutum* occurring primarily east of 110°W longitude and *T. platneri* generally found to the west (Pinto 1999). Although these are the dominant naturally occurring egg parasitoids of tortricid pests in fruit orchards, at least nine other native *Trichogramma* species also occur on these hosts (Pinto et al., in prep.). One of these, *T. californicum,* is a western species occurring in sympatry with *T. platneri.*

Trichogramma californicum was described from specimens reared from eggs of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnogh), collected from Alturas, Modoc Co., in northeastern California (Nagaraja and Nagarkatti 1973). In addition to this lymantriid it has been recorded from eggs of several species of Lycaenidae, and two species of Tortricidae, including *Cydia pomonella* (L.), the codling moth, one of the primary hosts of the *T. minutum* complex (Pinto 1999). *Trichogramma californicum* is not a common species but its range does overlap broadly with *T. platneri* in the western United States (Pinto 1999), and both have been taken from codling moth on apple in Idaho and northern California. *Trichogramma californicum* and members of the *Trichogramma minutum* complex are similar morphologically, separated by minor differences in color and structure. Sympatry and the occurrence of at least limited character intermediacy suggested the possibility of interspecific hybridization between *T. californicum* and *T.*

Table 1. Collection localities and generation of cultures examined in electrophoretic and crossing studies.

Species	Acronym	Collection Site	Laboratory Generation Studied
T. californicum	CASB	San Bernardino Mts, CA	>55
	CAAD	Adin, Modoc Co., CA	>175
	CAYK	Yakima, WA	>55
T. minutum	MCVA	Chula Vista, San Diego Co., CA	>675
T. platneri	PRV1	Riverside (UCR Campus), CA	>475
T. exiguum	EXSL	Selma, AL	>500
	EXHN	Hendersonville, NC	>60

platneri in the west. Although reproductive crosses of *T. californicum* showed complete incompatibility with several similar species including *T. platneri* (Pinto 1999), these results were based on single crosses, each involving no more than 20 pairs in each direction.

This paper investigates the distinctness of *T. californicum* and members of the *T. minutum* complex with further reproductive compatibility tests and allozymic electrophoresis. A large number of crosses were performed between three lines of *T. californicum* and *T. platneri* to determine if cases of morphological intermediacy could be explained by a degree of reproductive compatibility. We also include the eastern North American *T. exiguum* Pinto and Platner in this study because of its similarity to the *T. minutum* complex and, in particular, to *T. californicum* (Pinto 1999). *Trichogramma exiguum* also is known from codling moth and other fruit tree tortricid pests. It has frequently been taken on these hosts at localities that also harbor *T. minutum* (Pinto et al., in prep.). The interspecific studies presented here are similar to those performed between members of the *T. minutum* complex (Pinto et al. 1991, 1992), and on the closely related species pairs *T. deion*/*T. pretiosum* (Pinto et al. 1993) and *T. deion*/*T. kaykai* (Pinto et al. 1997).

MATERIALS AND METHODS

Cultures.—Cultures from three geographically distant populations of *T. californicum* were available for study. They were initially identified using morphology, and this was supported by their nearly identical ITS2 ribosomal transcript sequences (R. Stouthamer, pers. comm.). All are assignable to Form A of this species as defined by Pinto (1999). We utilized our standard laboratory cultures of *T. minutum* and *T. platneri* (Pinto et al. 1991), and two cultures of *T. exiguum*. The origin of all cultures used is given in Table 1. Cultures were collected and maintained as detailed in Pinto et al. (1991). Each originated from a single mated female that emerged from a field-collected host egg, and was maintained in the laboratory at 21–27° C on irradiated *Trichoplusia ni* (Hübner) eggs. Slide-mounted vouchers of all cultures studied are on deposit in the collection of the University of California, Riverside, Department of Entomology Research Museum, and are labelled with the voucher code RB1 and numbers UCRC ENT 43850–43984.

Crosses.—The three cultures of *T. californicum* were crossed with each other, with standard cultures of *T. platneri* (PRV1) and *T. minutum* (MCVA) that were used in previous studies (Pinto et al. 1992, 1993), and with the Hendersonville (EXHN) culture of *T. exiguum* for a total of ten crosses. The PRV1 and MCVA standard cultures have each been shown to be reproductively compatible with numerous other conspecifics (Pinto et al. 1992, in prep.). Procedures used for crossing experiments are detailed in Pinto et al. (1991). A single cross between two cultures consisted of an equal number of heterogamic (males from the other culture) and homogamic (males from the same culture) replicates. Each replicate consisted of a single virgin male and a single virgin female in a 29.6 cc (8 dram) glass vial with many (40 or more) host eggs. The male and female progeny from each replicate were counted, and the mean sex ratio (msr) for the cross calculated as the percentage of female progeny. The number of heterogamic and homogamic replicates of each cross were designed to number from 12 to 20 each, but fewer were performed in some cases due to extremely poor viability of certain *T. californicum* cultures. A total of 296 pairs of *T. californicum* and *T. platneri* were crossed to increase the chance of detecting rare hybridization. This included an expanded number of heterogamic crosses conducted in both directions between PRV1 × CAAD and PRV1 × CASB, and 39 between PRV1 × CAYK (Table 2). For statistical analyses, however, only the first 20 replicates were compared with the homogamic replicates. For each cross, an additional 10 virgin females were placed individually into separate vials with host eggs but without males to confirm that cultures were arrhenotokous.

Reproductive compatibility of a cross in each direction is expressed as a percentage: 100% × msr (heterogamic combination)/ msr (homogamic combination) (Fig. 1). In arrhenotokous *Trichogramma,* females hatch only from fertilized eggs, while males hatch from unfertilized eggs. The absence of female progeny indicates complete incompatibility. Relative degrees of compatibility were measured using the non-parametric Mann-Whitney U test to compare the mean sex ratio of the heterogamic crosses with that of the homogamic crosses (Sorati et al. 1996).

Electrophoresis.—A total of 14 enzyme systems were examined in the three cultures of *T. californicum,* the two reference cultures of *T. minutum* and *T. platneri,* and one of the two cultures of *T. exiguum* (Table 3). The enzyme systems, their Enzyme Commission numbers, and the abbreviations representing them in this paper are: aconitase (4.2.1.3) *Acon,* acid phosphatase (3.1.3.2) *Acp-2,* esterase (3.1.1.1) *Est-1,* fumarase (4.2.1.2) *Fum,* glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12) *Gapd,* α-glycerol-phosphate dehydrogenase (1.1.1.8) α*Gpd-1* and α*Gpd-2,* glucose-phosphate isomerase (5.3.1.9) *Pgi,* glucose-6-phosphate dehydrogenase (1.1.1.49) *G6pd, B*-hydroxybutyrate dehydrogenase (1.1.1.30) *Hbdh,* hexokinase (2.7.1.1) *Hk,* isocitrate dehydrogenase (1.1.1.42) *Idh,* malate dehydrogenase (1.1.1.37) *Mdh-2,* malic enzyme (1.1.1.40) *Me,* phosphoglucomutase (2.7.5.1) *Pgm.* The same culture (EXHN) of *T. exiguum* used for crosses could not be used for all loci because of a shortage of available specimens. The scores of another *T. exiguum* culture from Selma, AL (EXSL) were substituted for *Est-1, Me,* and *Pgi.*

The electrophoretic analysis followed procedures reported in Pinto et al. (1992), originally detailed in Kazmer (1991). Whole females, four from each culture per run, were individually analyzed at each locus by isoelectric focusing in one or two layers of cellulose acetate membranes using a single blend of carrier ampholytes (8% pH 4–6.5 and 2% pH 3–10 Pharmalytes), and an effective gel length of 4.5 cm.

BIOSYS-1 (Swofford and Selander 1989, release 1.7) was used to analyze the data. Nei's (1972) genetic distances (*D*) were calculated with individual allozyme profiles as input. All specimens were homozygous at the loci examined, probably due to the fact that each culture was established from a single mated female and because of the large number of generations that each culture had undergone prior to study (Table 1).

RESULTS

Crosses.—Results of the crossing studies are summarized in Fig. 1 and Table 2. Of the three crosses conducted among cultures of *T. californicum,* only that between

Table 2. Results of *Trichogramma* crosses conducted in this study.[1]

Heterogamic Crosses	No. Replicates	msr	Homogamic Crosses	No. Replicates	msr	*p*-value
CASB♂ CAAD	16	0.49	CAAD	16	0.62	0.2333
CAAD♂ CASB♀	8	0.67	CASB	8	0.43	0.0306*
CASB♂ CAYK♀	20	0	CAYK	20	0.59	—
CAYK♂ CASB♀	17	0	CASB	17	0.48	—
CAAD♂ CAYK♀	20	0	CAYK	20	0.68	—
CAYK♂ CAAD♀	20	0.19	CAAD	20	0.59	0.0001*
CASB♂ PRV1♀	20 (50)	0	PRV1	20	0.66	—
PRV1♂ CASB♀	20 (80)	0	CASB	20	0.66	—
CAAD♂ PRV1♀	20 (49)	0	PRV1	20	0.66	—
PRV1♂ CAAD♀	20 (78)	0	CAAD	20	0.33	—
CAYK♂ PRV1♀	19	0	PRV1	19	0.66	—
PRV1♂ CAYK♀	20	0	CAYK	20	0.59	—
CASB♂ MCVA♀	12	0	MCVA	12	0.65	—
MCVA♂ CASB♀	12	0	CASB	12	0.29	—
CAYK♂ MCVA♀	12	0	MCVA	12	0.70	—
MCVA♂ CAYK♀	12	0	CAYK	12	0.34	—
CASB♂ EXHN♀	12	0	EXHN	12	0.53	—
EXHN♂ CASB♀	12	0	CASB	12	0.49	—
CAYK♂ EXHN♀	12	0	EXHN	12	0.72	—
EXHN♂ CAYK♀	12	0	CAYK	12	0.48	—

[1] Numbers in parentheses indicate the actual number of replicates conducted in expanded crosses of *T. californicum* and *T. platneri,* with the accompanying number indicating the number of replicates used in the Mann-Whitney test. The *p*-value is that of the Mann-Whitney test, with those values significant at an α value of 0.05 indicated by an asterisk (*). Mean sex ratio (msr) is the average proportion of females in all replicates. See Table 1 for explanation of culture acronyms.

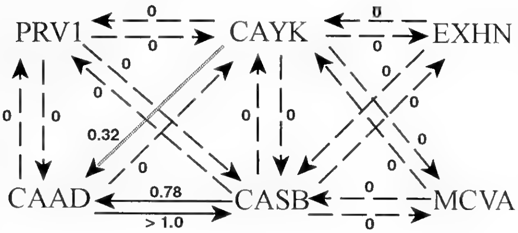

Fig. 1. Crossing results among cultures of *Trichogramma*. Solid arrows represent complete reproductive compatibility according to a Mann-Whitney U test. Dashed arrows represent complete incompatibility. Hatched arrows represent partial compatibility. Numbers along arrows represent level of reproductive compatibility for heterogamic cross relative to appropriate homogamic check cross. Arrows point to the parental female. See Table 1 for explanation of acronyms.

CAAD and CASB showed full bidirectional compatibility. Although the Mann-Whitney test indicated a significant difference between the homogamic check and the cross involving CAAD males and CASB females, the direction of significance was that of more females in the heterogamic cross. This difference is likely due to the generally poor viability of *T. californicum*. There was incomplete unidirectional compatibility between CAYK males and CAAD females as indicated by the Mann-Whitney test. Only 10 of the 20 CAAD females produced female progeny in this heterogamic cross, whereas 19 of the 20 CAAD females produced daughters in the homogamic check. The cross between CASB and CAYK was incompatible in both directions.

Table 4. Nei genetic distances (*D*) among cultures of *Trichogramma* examined electrophoretically.

Culture	CASB	CAYK	MCVA	PRV1	EXHN/ EXSL
CAAD	0.470	0.693	0.693	0.693	0.981
CASB	—	0.470	0.693	0.470	0.981
CAYK		—	0.981	0.693	1.386
MCVA			—	0.470	0.693
PRV1				—	0.625

None of the interspecific crosses yielded female progeny, including the relatively large number of replications between *T. californicum* and *T. platneri*. This is consistent with an earlier cross between CAAD and a collection of *T. platneri* from Cow Head Lake (Modoc Co.), CA (Pinto 1999). It is not known whether interspecific matings occurred or not.

Electrophoresis.—Of the 14 loci examined, eight showed variation (Table 3). No usable results were obtained with *Acon, Fum, Gapd, Hbdh, Hk,* or *Mdh.* The *T. californicum* cultures differed from those of the other species at three loci, *Acp-2, G6pd* and *Pgm,* although each of these loci was variable among cultures of *T. californicum* as well. Nei's genetic distance was calculated for the cultures analyzed in this study (Table 4), and the distances plotted in a phenogram using UPGMA clustering (Fig. 2). The distances and phenogram are intended as numerical and visual representations of the results, and should not be in-

Table 3. Allelic designation of 8 loci for the cultures examined.[1]

Species	Culture	*Acp-2*	α*Gpd-1*	*Est-1*	*G6pd*	*Idh*	*Me*	*Pgi*	*Pgm*
T. californicum	CAAD	D	A	C	C	B	A	A	B
	CASB	C	A	B	C	B	A	A	D
	CAYK	C	A	B	D	A	A	A	B
T. minutum	MCVA	A	A	null	B	B	A	A	C
T. platneri	PRV1	B	A	B	B	B	A	A	A
T. exiguum	EXHN	E	B	—	A	B	—	—	E
	EXSL	—	—	A	—	—	A	A	—

[1] Relative distances traveled for electromorphs at each locus expressed as a ratio of distance between edge of cathode and homomeric band to entire gel length in alphabetical order of allelic designation: *Acp-2* (0.42, 0.51, 0.58, 0.60, 0.62), α*Gpd-1* (0.22, 0.33), *Est-1* (0.07, 0.11, 0.20), *G6pd* (0.09, 0.22, 0.42, 0.47), *Idh* (0.58, 0.64), *Me* (0.49), *Pgi* (0.51), *Pgm* (0.11, 0.27, 0.29, 0.33, 0.58).

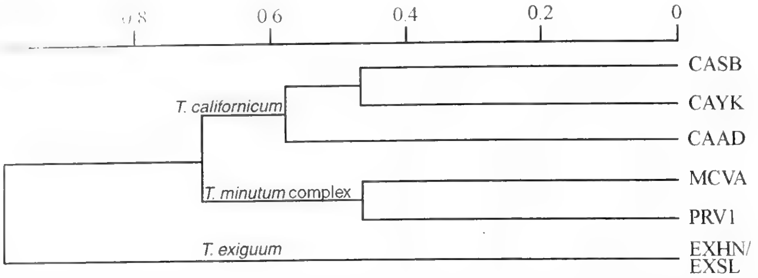

Fig. 2. Phenogram (UPGMA clustering) of Nei's genetic distances among cultures of *Trichogramma* examined electrophoretically. See Table 1 for explanation of acronyms.

terpreted phylogenetically. The phenogram does show the three cultures of *T. californicum* to be nearer to each other than to the cultures of the other species, but it should be noted that CASB is as near to PRV1 in the distance matrix as it is to either of the other homospecific cultures (Table 4).

The results for *Pgm* were compared with those reported for several cultures of the *T. minutum* complex (Pinto et al. 1992) using the results for MCVA and PRV1 as standards of comparison. Other than crossing unknowns with standard cultures, this locus provides the only means of separating most collections of *T. platneri* and *T. minutum* from one another. The electromorphs for *T. californicum* were different from all known *Pgm* electromorphs in the *T. minutum* complex and in *T. exiguum* (Table 3). The data for *Acp-2* and *G6pd* could not be compared with information from the prior study, but they are tentatively assumed to be diagnostic loci for *T. californicum.*

Discussion

The crossing and electrophoretic results provide no basis for explaining the morphological intermediacy previously found between *T. californicum* and *T. platneri.* Every one of the almost 300 reproductive pairings between the two species was negative. Also, the two species have distinct allozymic profiles, as well as different ITS2 sequences (van Kan et al. 1996). Speculation on causes other than gene flow for this intermediacy is premature and the basis of reproductive incompatibility between the species remains unknown.

The failure to detect reproductive or molecular intermediacy between *T. californicum* and *T. platneri* in this study, of course, could be explained by limited sampling. Although we failed to find hybridization in the numerous heterospecific pairings, the individuals of *T. californicum* and *T. platneri* crossed represent few isofemale lines (three and two, respectively). More extensive sampling would be useful. Utilization of isofemale lines unfortunately is necessary in *Trichogramma* studies to insure that all replicates are homospecific (Pinto et al. 1992). The preferable approach of utilizing unrelated individuals for replications is precluded by the presence of heterospecifics at most collection sites (potentially in the same host egg) coupled with problems of identification. In *Trichogramma,* females can not be identified unless associated with males, and slide-mounted material is required for male identification. Genetic variation could be better estimated by utilizing a larger number of isofemale lines, but this alternative is not straightforward in uncommon species such as *T. californicum.*

The limitations of our sampling procedure notwithstanding, it should be noted that the species of *Trichogramma* studied reproductively thus far indicate that the magnitude of morphological difference separating *T. californicum* and the *T. minutum* complex, as minor as it is, does correlate well with reproductive incompatibility (Pinto 1999). If the few cases of intermediacy are due to hybridization we predict that they result from relatively uncommon events. We also should mention that although few *T. californicum* lineages have been studied allozymically thus far, the *Pgm* locus has been examined in over 100 lineages of the *T. minutum* complex (Pinto et al., in prep). In all cases, the alleles at this locus in both species of the complex are distinct from those reported here for *T. californicum.*

Both crossing and electrophoretic results indicate a high degree of intraspecific variation in *T. californicum* as compared to that found in certain other species of *Trichogramma* (Pinto et al. 1992, 1993). The greatest Nei's distance found among the three cultures of *T. californicum* (0.693) is far greater than distances reported in all species of *Trichogramma* analyzed to date (Pinto et al. 1992, 1993), including that found in *T. minutum* (0.486). In fact, the least distance between cultures of *T. californicum* (0.470) is greater than the greatest distance between cultures of all other species previously examined except *T. minutum.* These allozymic differences are not predicted by the bidirectional reproductive compatibility between the Adin and San Bernardino cultures of *T. californicum,* or the partial compatibility between the Adin and Yakima cultures. They also are not predicted by known morphological or ITS2 sequence similarity. ITS2 sequences are useful in separating all morphologically distinctive species examined thus far (Stouthamer et al. 1999), but are nearly identical in the three *T. californicum* cultures (Stouthamer, pers. com.). The degree of reproductive disjunction within *T. californicum,* however, is not completely without precedence in *Trichogramma.* Pinto et al. (1991) found similar levels of incompatibility among cultures of *T. deion.* They also reported one-way incompatibility and reduced two-way compatibility in cultures currently assigned to *T. minutum.*

Considerable morphological variation within *T. californicum* already has been noted and the species was divided into two forms, A and B, on this basis (Pinto 1999). The two are broadly sympatric in California but Form B is known only from museum specimens. Within Form A, populations from Baja California and western Texas also have been identified as morphological outliers (Pinto 1999). Crossing and molecular studies are needed to determine their relationship to the cultures investigated here. Clearly, *Trichogramma californicum* remains a highly variable and poorly understood entity. It may constitute a unit of variation similar to or greater than the *T. minutum* complex where the two component species also are morphologically similar but reproductively incompatible. As in *T. californicum,* these reproductive units (*T. minutum* and *T. platneri*) are electrophoretically distinct (Pinto et al. 1992) but do not differ in ITS2 sequence (Stouthamer et al. 2000). However, species status for *T. minutum* and *T. platneri* also has been supported by clear-cut reproductive incompatibility and distinct geographic distributions. The geography of reproductive incompatibility and allozymic variation in *T. californicum* is unknown and any proposal to subdivide the species without more extensive sampling is premature.

ACKNOWLEDGMENTS

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A NEW SPECIES OF *MAEVIUS* STÅL FROM AUSTRALIA AND SOME NOTES ON THE FAMILY HYOCEPHALIDAE (HEMIPTERA: HETEROPTERA)

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Abstract.—***Maevius luridus*, n. sp.,** is described from Australia and compared with *Maevius indecorus* Stål, the only previously known species of the genus. Habitus view illustrations and drawings of the male genitalia are provided to distinguish the three species now included in the family Hyocephalidae. New records for *Hyocephalus aprugnus* Bergroth and *Maevius indecorus* are presented. A key to the genera and species is given.

Key Words: Hemiptera, Hyocephalidae, *Maevius, Hyocephalus,* taxonomy

The endemic Australian family Hyocephalidae has both Coreidae and Lygaeidae features and is perhaps the most primitive of the families of the Coreoidea (Stys 1964; Schaefer 1964, 1965, 1981). Previously two genera and two species were known. The first hyocephalid, *Maevius indecorus,* was described by Stål (1874) from Moreton Bay in Queensland, Australia, and was included in the Division Lethaearia of the Family Lygaeidae. Scudder (1962) removed the genus *Maevius* from the Lygaeidae and transferred it to the Coreidae because of its external similarity to *Lygaeopharus* Stål (Coreidae: Colpurini). Bergroth (1906) described the second taxon, *Hyocephalus aprugnus,* from a single macropterous female from South Australia (Yorketown) and included this genus in a new subfamily, Hyocephalinae, within the Coreidae. Later Bergroth (1912) described a brachypterous female from New South Wales, Australia, and reduced the rank of this group to a mere division (Hyocephalaria) of the Coreidae. Reuter (1912) raised Hyocephalinae to family rank and this action has been followed by all subsequent authors. Stys (1964) in the only previous comprehensive paper on the Hyocephalidae retained them as a family, giving a detailed description, and distinguishing them from Coreidae, Largidae, Lygaeidae, Stenocephalidae and Pyrrhocoridae. In that seminal contribution only *Hyocephalus aprugnus* was available for study.

Kumar (1965) analyzed the position of the hyocephalids, and concluded that the type of ovipositor in this family is a modification in response to its particular mode of life. A year later Kumar (1966) studied the biology, the immature stages and the relative growth of some Australian bugs. The species studied by Kumar in both papers under the name *Hyocephalus* sp. nov. was actually *Maevius indecorus.*

Recently Schuh and Slater (1995) summarized the general morphology of the Hyocephalidae.

In this paper I describe a second species of *Maevius* and give new distributional records for the other two species in the family.

The following abbreviations indicate institutions where specimens are deposited or which generously lent material: Australian

National Insect Collection, Canberra (ANIC); The Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); Colección Entomológica del Instituto de Biología, Universidad Nacional Autónoma de México (UNAM); James A. Slater Collection (JAS); Australian Museum, Sydney (AMS); Queensland Museum, Brisbane (QMBA); South Australian Museum, Adelaide (SAMA); University of Queensland Insect Collection, Brisbane (UQIC); Western Australian Museum, Perth (WAM).

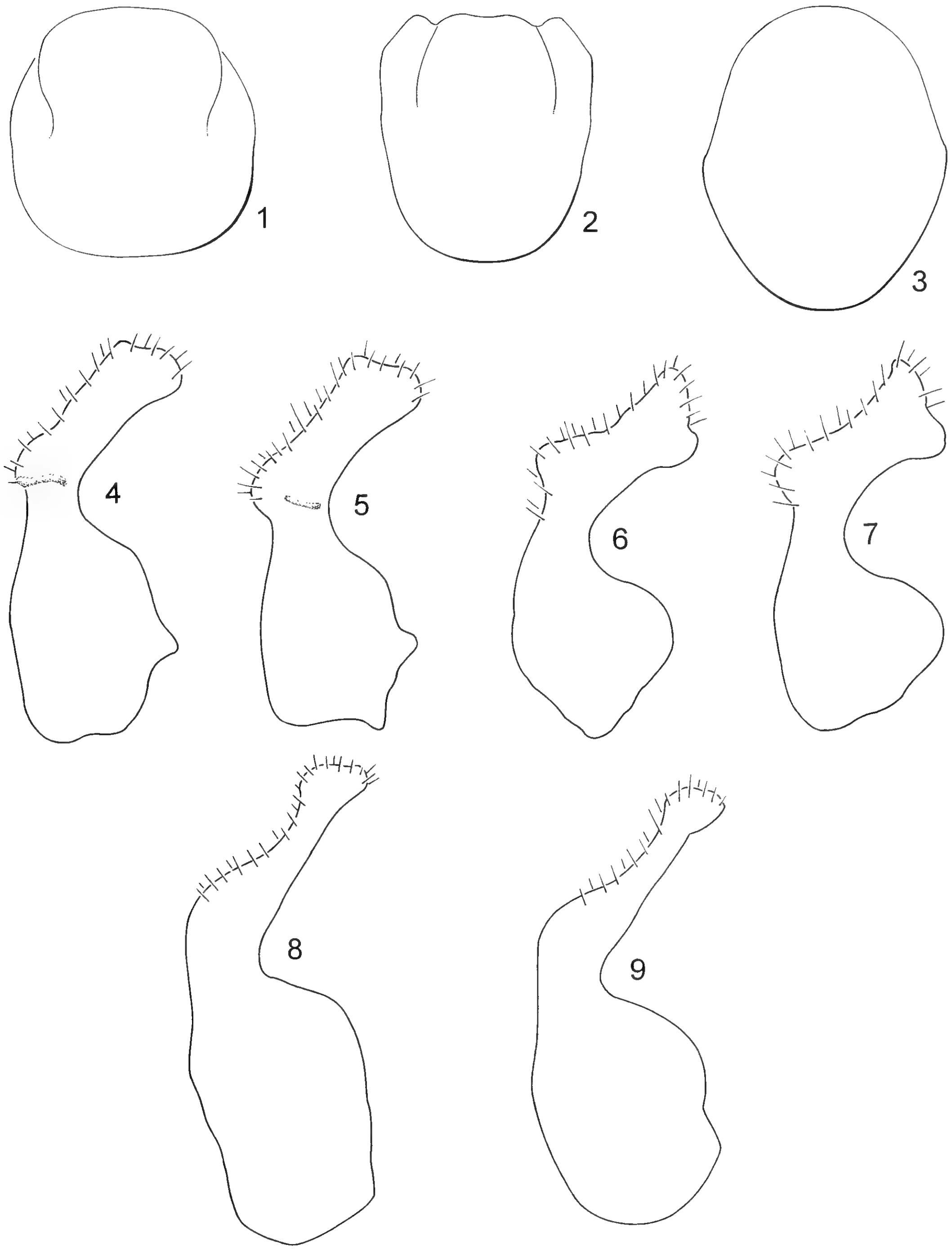
All measurements are given in millimeters.

Maevius luridus Brailovsky, new species

(Figs. 1, 4, 5, 11)

Description.—*Measurements:* Male first, female second: Head length: 1.70, 1.89; width across eyes: 1.27, 1.30; interocular space: 0.80, 0.81; interocellar space: 0.59, 0.62; preocular distance: 1.30, 1.36; length antennal segments: I, 1.42, 1.39; II, 1.45, 1.55; III, 0.77, 0.78; IV, 0.89, 0.92. Pronotum: Total length: 1.42, 1.48; width across frontal angles: 1.30, 1.37; width across humeral angles: 1.98, 2.01. Scutellar length: 1.08, 1.20; width, 1.33, 1.36. Total body length: 9.10, 10.20.

Male: *Dorsal coloration:* Head brown on ochre yellow background, with space between eye and ocelli and a median longitudinal band running from apex of tylus to vertex light yellow; antennal segments I to III black, and IV yellow with basal third black; pronotum, scutellum, clavus and corium ochre yellow with light brown mottled patches; connexival segments III to VI light brown with anterior and posterior third yellow, and VII light brown with posterior third yellow; dorsal abdominal segments I to VI yellow with middle third of each segment black, and VII ochre yellow with light brown mottled patches. *Ventral coloration:* Head including rostral segments I to IV yellow, with basal third of rostral segment II and median gular region brown; thorax light brown on ochre yellow background, with acetabulae, and metathoracic peritreme yellow; legs ochre yellow; abdominal sterna yellow with light brown mottled patches; pleural margin of abdominal sterna III to VI light brown with anterior and posterior third yellow, and VII light brown with posterior third yellow. *Sculpture:* Head, pronotum, scutellum, corium, clavus, thorax, and abdominal sterna dull, with small tubercles, bearing short, minute, curved-like hairs; antennal segments densely covered with adpressed golden setae, with some semierect longer setae, denser on segments II to IV; femora with few scattered setae; tibiae with some minute, adpressed, hardly recognizable hairs, and with many longer, straight setae; both ventral edges of tibiae bear one row of spine-like, thicker setae; tarsi densely covered with long setae, especially on ventral surfaces. *Structure:* Head horizontal, porrect, very long and narrow; postocular section thicker than anteocular one; frons and vertex convex; eyes small, remote from pronotal margin; ocelli very small, situated near posterolateral eye margin; tylus elevated, narrow, laterally compressed, anteriorly considerably surpassing jugae; jugae short, and anteriorly pointed; antenniferous tubercle distinctly infericorn in position, remote from eyes, occupying nearly whole area between gula and tylus, large with divergent and convex lateral sides, simple anterolateral corners, and very large apical membraneous sockets; bucculae large and long, anteriorly rounded, gradually narrowing posteriorly, disappearing at level anterior eye margin; rostrum reaching anterior border of mesosternum. *Pronotum:* Trapezoidal; collar evident; frontal angles distinctly produced anteriorly; lateral margins weakly sinuate, emarginate; humeral angles slightly exposed; posterior margin weakly straight; disc with a pair of indistinct large, oval callar impressions. *Legs:* Fore femur ventrally armed with a double row of subapical spines; middle and hind femora unarmed; tibiae sulcate. *Scutellum:* Triangular; disc almost flat; anterolateral corners with a pair of irregular depressions;



Figs. 1–9. 1–3, Male genital capsule in caudal view. 1, *Maevius luridus*. 2, *Maevius indecorus*. 3, *Hyocephalus aprugnus*. 4–9, Parameres in lateral view. 4, 5, *Maevius luridus*. 6, 7, *Maevius indecorus*. 8, 9, *Hyocephalus aprugnus*.

apex sub[illegible] *[illegible]lytra:* Staphylinoid; clavus and corium indistinguishably fused into a [illegible] pad, and hemelytra meeting each other along midline for their entire length; posterior end truncated and covering only first three abdominal terga; hemelytral membrane absent. *Abdomen:* Connexival segments higher than terga; connexival margin complete; posterior angle of each connexival segment complete, not extending as a short spine. *Genitalia:* Genital capsule with posteroventral margin complete; surface convex, laterally slightly raised almost for their whole longitudinal length (Fig. 1). Paramere as in Figs. 4–5.

Female: *Coloration:* Similar to male. Genital plates brown with upper margin yellow. *Structure:* Abdominal sternite VII fissured for their entire length; paratergite VIII short, squarish, with visible spiracle; paratergite IX larger, square; II valvifers narrow, parallel and interlocking at their entire length.

Variation (in both sexes).—1, Antennal segment I chestnut orange. 2, Connexival segments III to VII with upper margin brown, lower margin chestnut orange, and anterior and posterior third yellow to ochre yellow. 3, Trochanters light chestnut orange.

Type material.—Holotype: ♂, Australia: South Australia, Eyre Penn., near Caralue Bluff, under Spinifex sp. (Gramineae), 8 October 1964, F. J. Mitchel (SAMA). Paratypes: 1 ♀, same data as holotype (SAMA); 2 ♂, 1 ♀, Australia: Arden Vale, on Triodia sp. (Gramineae), 19 June 1976, C. van Dyk (SAMA, UNAM); 1 ♂, 1 ♀, Australia: Victoria: Hattah Lakes Nat. Park, 4 April 1969, G. B. Monteith, (QMBA).

Diagnosis.—This is a medium-sized species similar to *M. indecorus* Stål, the only previously known species of the genus. *Maevius luridus* is easily distinguished by the pale ochre yellow coloration in contrast with the dark reddish brown coloration of *M. indecorus* on which only the following areas are pale yellow or chestnut orange: antennal segment IV, anterior and posterior third of abdominal terga III to VII, trochanters, basal third of tibiae, tarsi, and anterior and posterior third of pleural margins of abdominal sterna III to VII. The length of antennal segments I to IV are shorter in *M. luridus* and the shape of the parameres also differs (Figs. 4–7).

Distribution.—Known only from the Southeastern part of South Australia and the Northwestern of Victoria.

Etymology.—Named for its light coloration; from the latin *luridus,* pale yellow.

Maevius indecorus Stål
(Figs. 2, 6, 7, 10)

Maevius indecorus Stål 1874: 165.

The morphology and life history of this species were studied by Kumar (1965, 1966) under the name *Hyocephalus* sp. nov. He mentioned that it probably feeds on the seeds of *Acacia* (Leguminosae) or *Eucalyptus* (Myrtaceae), or both.

Distribution.—Stål (1874) described this species from Moreton Bay in Queensland, Australia. Kumar (1966) recorded it from Moggill, near Brisbane. The new records listed below show it occurs from Rockhampton south to Newcastle in Eastern Australia and in the Southeastern Western Australia.

Material examined.—Australia: Queensland: 1 ♂, 1 ♀, S. E. Queensland: Brisbane, Rochedale, January 1980, V. Davies and R. Raven (UQIC, QMBA); 2 ♂, Lamington Nat. Park, 17–24 May 1965, G. Monteith (UQIC); 1 ♂, Mt. Chalmers, 24 October 1990, R. Raven (QMBA); 1 ♂, 4 ♀, Bunya Mts., 27–31 May 1962, E. A. Bernays, 17–18 September 1966, G. Monteith (UQIC); 1 ♂, 2 ♀, Dunwich Stradbroke Is., 9 May 1964, 15–16 March 1975, 21 April 1965, G. Monteith (UQIC); 1 ♀, Big Sand Hill at Moreton I., 1 October 1955, E. N. Marks (from litter under *Banksia*) (UQIC); 1 ♀, Dunwich, 11 April 1965, J. E. Dunwoody (UQIC); 1 ♂, Fletcher, without date, E. Sutton (UQIC); 1 ♂, thunderbird Park (Tamborine Mts.), 23–29 October 1993, S. A. Slipinski and J. F. Lawrence (ANIC); 2 males, 1 female, Brisbane, adults taken at Moggill on banks of River Brisbane and

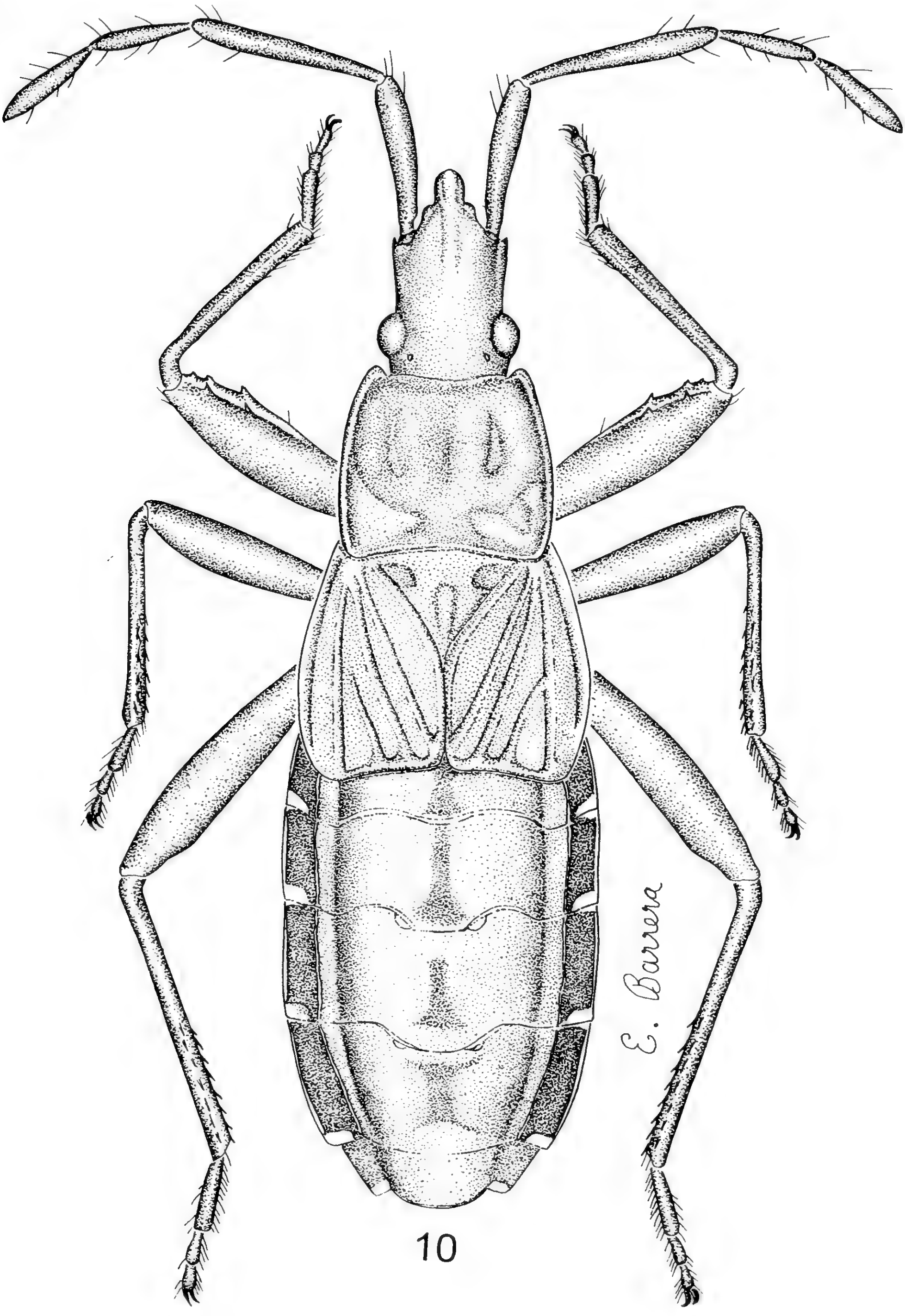


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Fig. 10. Dorsal view of *Maevius indecorus*, male.

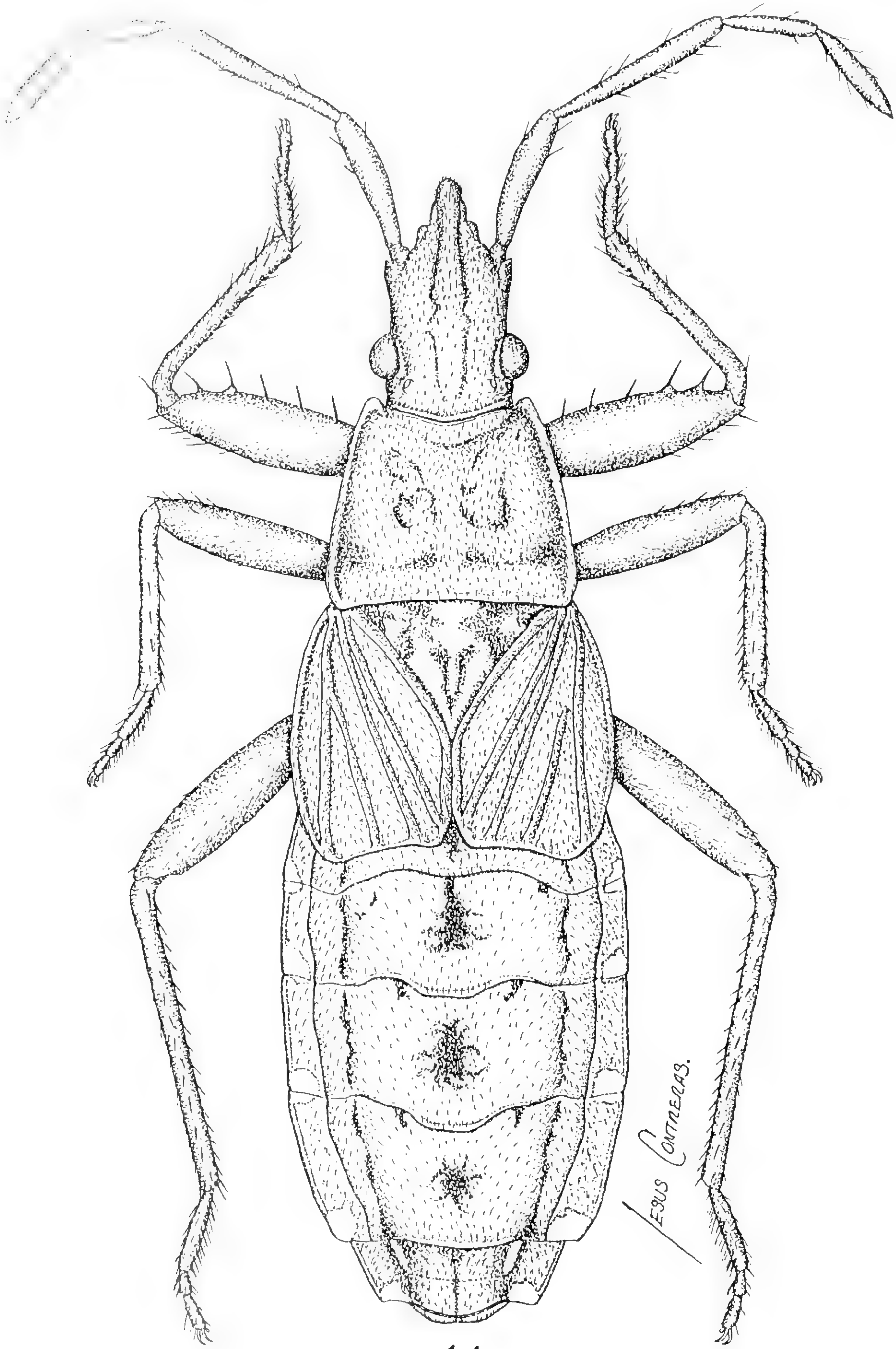

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Fig. 11. Dorsal view of *Maevius luridus*, male.

reared in culture by R. Kumar (BPBM); 20 ♂, 35 ♀, Brisbane, 20 May 1960, H. A. Rose, 19 August 1960, M. Smith, 15 October 1963, December 1963, R. Kumar, 1–9 January 1964, R. Kumar, 17 December 1964, R. Kumar (BPBM, UQIC, UNAM); 5 ♂, 4 ♀, Moggill, 2 April 1962, T. E. Woodward, 7–16 September 1963, R. Kumar, 4 October 1963, R. Kumar (UQIC); 1 ♀, Blackdown Tableland, via Dingo, 1–6 February 1981, G. B. Monteith (QMBA); 4 ♀, Highvale, March 1970, B. Cantrell (UQIC); 1 ♀, Brisbane, Mt. Coot-tha, 10 January 1972, J. A. Slater (JAS). Australia: New South Wales: 1 ♂, Greta, 1951, J. Sedlacek (BPBM); 2 ♂, 2 ♀, Unumgar State Forest, via Kyogle, 12 April 1966, G. Monteith (UQIC); 1 ♀, Bonie N., Coonabarabran, 6 September 1970, B. Cantrell (UQIC); Western Australia: 1 ♀, Goldfields Surv., Lake Cronin, 5 June 1981, W. F. Humphreys (WAM); 3 ♀, Wildlife Res., 21 mi., N. of Perth, 16 December 1971, J. A. Slater (adults taken under *Hypocalymna angustifolium* Endl. (Myrtaceae) (JAS, UNAM); 1 ♀, Mt. Cooke, 43 mi., S. of Perth, 23 March 1968, F. H. Uther Baker (SAMA); 1 ♀, 2 mi., W. of Fraser Range, 3 June 1979, F. W. Aslin (adult taken under road side rocks on edge of old road) (WAM); 2 ♂, Stirling Range, 4 March 1994, Monteith and Janetzki (QMBA).

Hyocephalus aprugnus Bergroth
(Figs. 3, 8, 9, 12, 13)

Hyocephalus aprugnus Bergroth 1906: 648.

Bergroth's (1906) original holotype was considered lost for many years and when Stys (1964) discovered 11 specimens clearly collected with the holotype in the Hungarian Natural History Museum he designated one as a neotype. Later the original holotype was discovered in the University Zoology Museum Helsinki but Grant and Stys (1970) applied for retention of the neotype.

Stys (1964) characterized the genus and the species and commented on the morphology and relationship of the group. The macropterous (Fig. 13) and staphylinoid (Fig. 12) condition, has been adequately redescribed by Bergroth (1912) and Stys (1964).

Distribution.—This species was described from Yorketown (near Adelaide) in South Australia (Bergroth 1906), and later recorded from an unspecified locality in New South Wales (Bergroth 1912). The new records listed below show it occurs in the Southwestern Western Australia and in the Southeastern corner of Western Australia. No material is available to confirm its occurrence in New South Wales.

Material examined.—Australia: South Australia: 1 ♂, 1 ♀, Gum Lagoon 36°17′S–140°02′E, 25 March 1992, J. A. Forrest (SAMA); 1 ♀, 9 km., N. of Long Point, 35°37′S–139°39′E, 5–9 September 1991 (SAMA); 1 ♂, Loftia Park, 21 September 1989, D. Hirst (SAMA); Western Australia: 1 ♀, Torbay in Let, 10 mi., W. of Albany, 28 December 1971, J. A. Slater (JAS); 1 ♀, Mt. Cooke, 43 mi., S of Perth, 23 March 1968, F. H. Uther Baker (WAM); 1 ♂, Limestone Head, via Albany, 3 March 1970, G. W. Kendrick (UNAM); 1 ♂, 1 ♀, Garden Island, 32°12′S–115°40′E, 18 June 1969, B. Humphreys (adult taken under galvanized iron at the base of *Pittosporum* (Pittosporaceae) and 12 November 1975, S. M. Slack Smith (WAM); 1 ♂, Vicinity of Devils Lair Cave, near Karridale, 20 March 1973, A. Baynes (UNAM); 1 ♂, 1 ♀, White Gum Flat, Stirling Range Nat. Park, 34°24′S–117°55′E, 1 April 1993, M. S. Harvey and J. M. Waldock (WAM); 2 ♂, 3 ♀, Thomas R., Cape Arid, 23 May 1977, R. McMillan (UNAM, WAM).

PLANT ASSOCIATIONS

Hyocephalids live on the ground in a variety of habitats from semi-desert to tall coastal eucalypt forest. They shelter under stones, logs and other debris. *Maevius indecorus* has been taken under the prickly hummocks of *Spinifex* (*Triodia* spp.) grasses, a specialized Australian desert habitat occupied

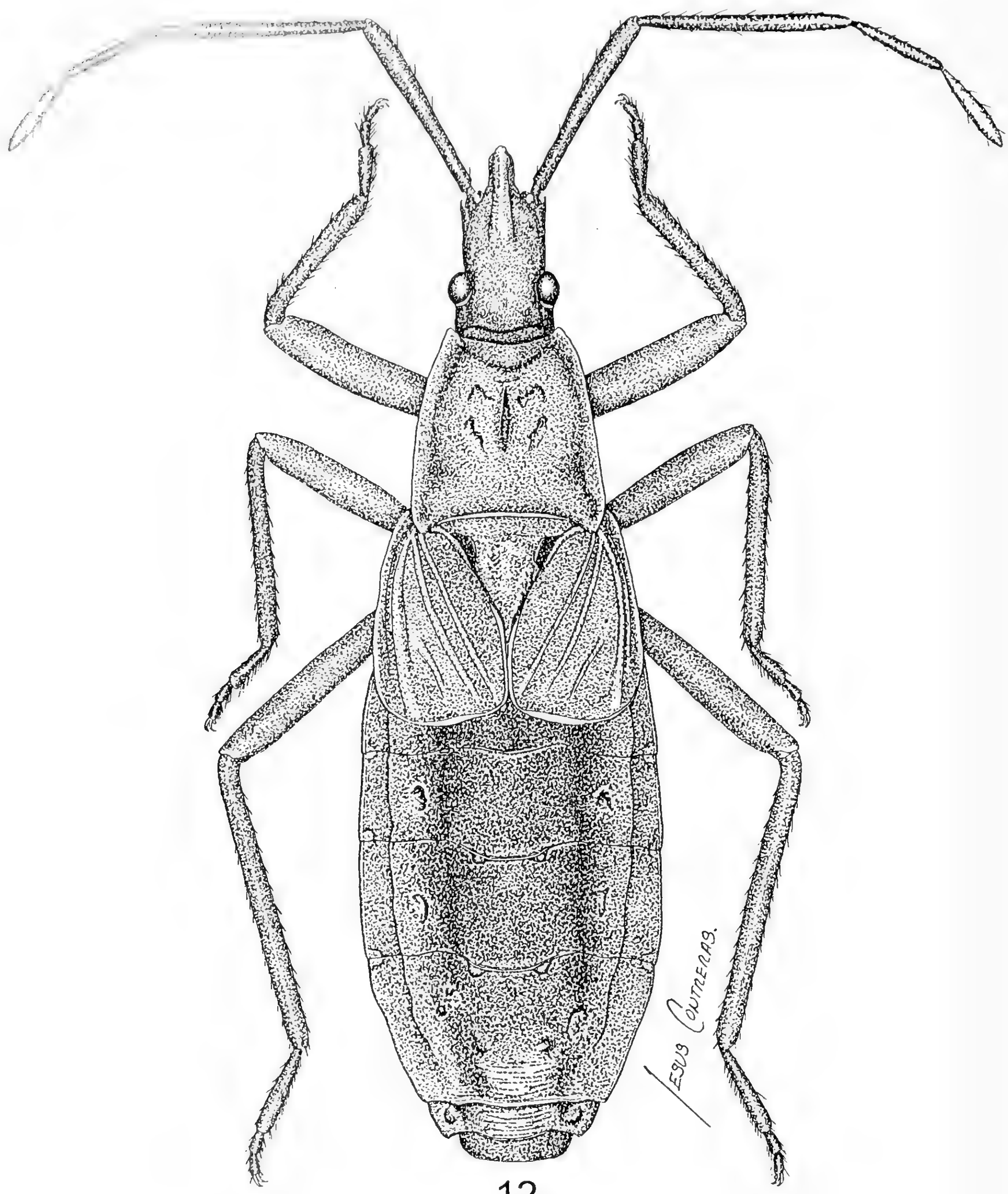

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Fig. 12. Dorsal view of *Hyocephalus aprugnus,* male staphylinoid.

by many invertebrates (Monteith, pers. comm.).

The natural food of hyocephalids has not been recorded but is assumed to be seeds. Kumar (1966) successfully reared *Maevius indecorus* through several generations in the laboratory on sunflower seeds. He speculated that they may feed on seeds of *Eucalyptus* (Myrtaceae) and *Acacia* (Mimosaceae) in nature. This speculation was repeated as fact (Schaefer and Mitchell 1983, Schuh and Slater 1995) but has not been

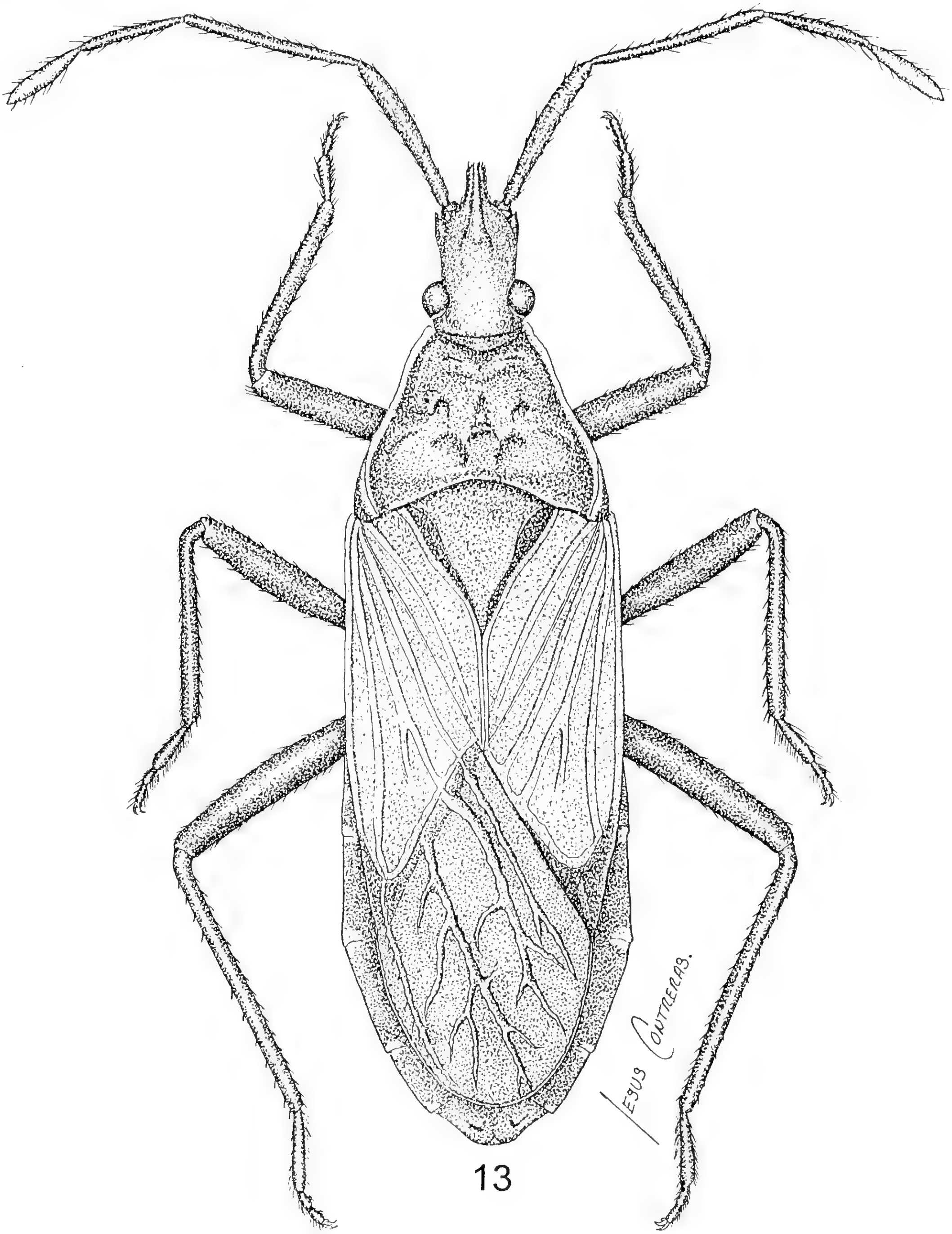

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Fig. 13. Dorsal view of *Hyocephalus aprugnus,* female, macropterous.

confirmed. Label data on specimens reported in this paper record *Maevius indecorus* in association with *Hypocalymna angustifolius* Endl. (Myrtaceae) and *Banksia* (Proteaceae). *M. luridus* in association with *Spinifex* and *Triodia* (Gramineae) and *Hyocephalus aprugnus* in association with *Pittosporum* (Pittosporaceae). No direct feeding can be assumed from any of these.

Key to the Known Species of Hyocephalidae

1. Antennal segment III longer than IV; fore femur unarmed or with some subapical tubercles; antennal segment I longer than 1.95 mm; parameres like Figs. 8–9 . . . . *Hyocephalus aprugnus* Bergroth
– Antennal segment III shorter than IV; fore femur armed with double row of apical spines; antennal segment I shorter than 1.80 mm; parameres like Figs. 4–7 2
2. Body dark reddish brown; antennal segment I slender and longer than 1.68 mm; parameres like Figs. 6–7 . . . . *Maevius indecorus* Stål
– Body ochre yellow or pale brown on a ochre yellow background; antennal segment I robust and shorter than 1.60 mm; parameres like Figs. 4–5 . . . . *Maevius luridus,* n. sp.

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PERLESTA ETNIERI (PLECOPTERA: PERLIDAE), A NEW SPECIES OF STONEFLY FROM TENNESSEE

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ABSTRACT.—A new species of stonefly, ***Perlesta etnieri*** is described from Maury and Williamson counties, Tennessee. It is a member of the *nelsoni* species group but can be distinguished from included species by the absence of two well-defined patches of sensilla basiconica on tergum 10 and by the dark body coloration. Additionally, new Tennessee state records are reported: *P. adena* Stark (Sumner, Trousdale, and Williamson counties) and *P. lagoi* Stark (Bledsoe and Cumberland counties).

Key Words: Plecoptera, Perlidae, *Perlesta,* new species

The stonefly genus *Perlesta* now rivals *Neoperla* and *Acroneuria* in numbers of species in North America, a remarkable fact considering that during most of the 20th century only a single widespread species was recognized (Stark 1989). Currently, seventeen species are recognized (Stark 1989, Poulton and Stewart 1991, Stark and Rhodes 1997, Kirchner and Kondratieff 1997, DeWalt et al. 1998, Kondratieff and Baumann 1999). Recently, DeWalt et al. (2001) reviewed the *Perlesta* of Illinois, documenting eight species for the state.

A new species of *Perlesta* was discovered among material from Tennessee submitted for identification by Dr. David A. Etnier, University of Tennessee. The authors collected additional adult material from the Harpeth River. This species is described below. The descriptive terminology follows Stark (1989).

Perlesta etnieri Kondratieff and Kirchner, new species

(Figs. 1–6)

Male.—Forewing length 8–9 mm. General body color black in life, brown in alcohol. Head yellow with black to brown ocellar patch and dark spot anterior to patch (Fig. 1). Wings black to brown except for pale costal margin. Femora yellow, distally and dorsally brown, tibiae brown with apices yellow. Abdominal terga black to brown, sterna yellow brown but darker brown apically. Cercus yellow basally, each segment posteriorly brown, distal segments brown. Tergum 10 mesal sclerite shiny dark brown, not divided, sensilla basiconica distinct but small, not elevated into patches (Fig. 2). Paraproct in lateral view, long, slender, slightly curved posteriad at apex, small mesoapical tooth (Fig. 3) not visible in caudal aspect. Penis tube + sac long, caecum absent (Fig. 4).

Female.—Forewing length 10–12 mm. Color pattern similar to male but paler. Sub-

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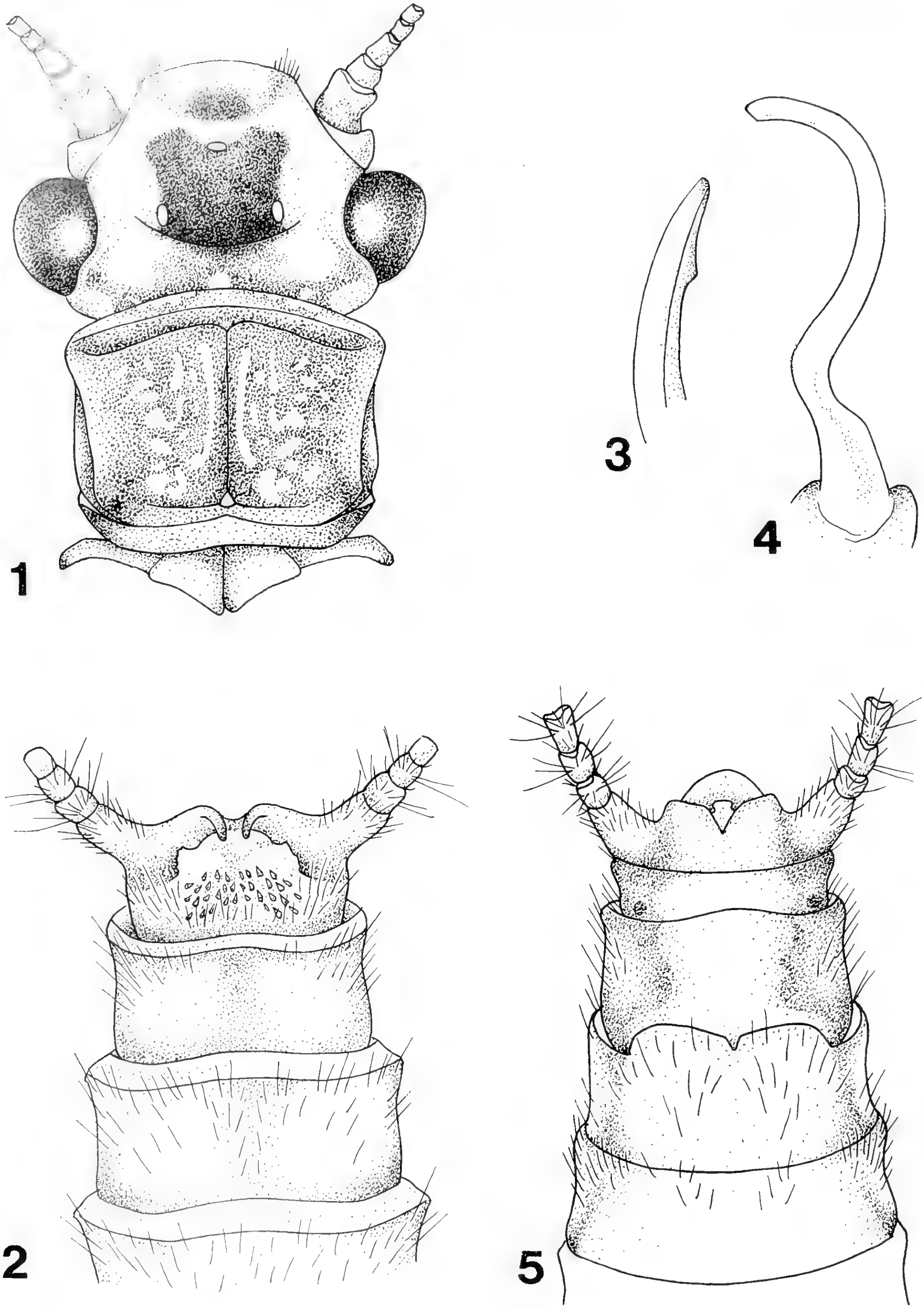
[1] The views of the author do not purport to reflect the position of the Department of the Army or the Department of Defense.



Figs. 1–5. *Perlesta etnieri.* 1, Adult head and pronotum. 2, Male terminalia, dorsal. 3, Paraproct, lateral. 4, Penis. 5, Female subgenital plate, ventral.

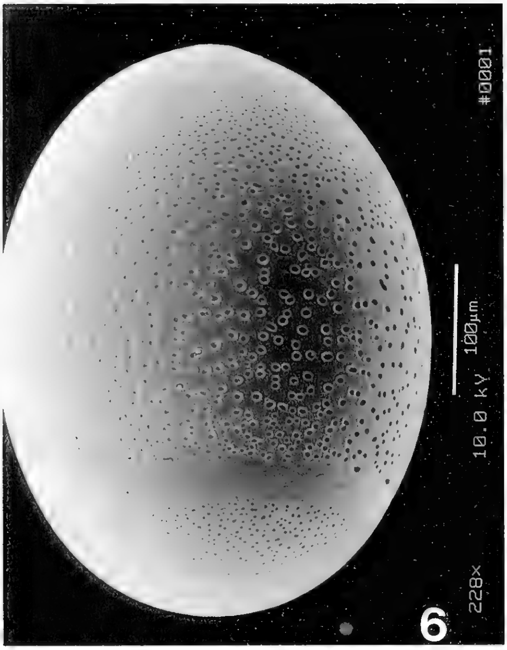


Fig. 6. *Perlesta etnieri.* Scanning electron photomicrograph of egg.

genital plate lobes short, truncate and separated by small V-shaped notch (Fig. 5).

Egg.—Collar sessile. Chorion surface covered with shallow irregular pits. Wide smooth eclosion line, with micropyles located at upper margin of line (Fig. 6).

Nymph.—Undescribed.

Material examined.—Holotype ♂, Tennessee, Williamson Co., Harpeth River at Millview, Arno Road (N35°52′41.0″ W86°47′27.1″), 11 May 2000, R. F. Kirchner and B. C. Kondratieff. Paratypes, same data as Holotype, 18 ♂, 4 ♀; same location but 19 May 1998, R. B. Evans, 46 ♂, 25 ♀; Maury Co., Carters Creek, at Carters Creek, Carters Creek Road (N35°43′02.7″ W86°59′44.7″), 19 May 1998, R. B. Evans, 32 ♂, 40 ♀.

The holotype is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. Paratypes will be deposited at the following museums and individual collections: Bill P. Stark, Clinton, Mississippi (BPS), C. P. Gillette Museum of Arthropod Diversity, Colorado State University (CSU), Illinois Natural History Survey (INHS), and Ralph F. Kirchner (RFK), Huntington, West Virginia.

Etymology.—We honor Dr. David A. Etnier, University of Tennessee, a well-known North American ichthyologist and trichopterist.

Diagnosis.—*Perlesta etnieri* belongs to a species group including *P. frisoni* Banks, *P. nelsoni* Stark, and *P. teaysia* Kirchner and Kondratieff, males of which are characterized by a long and slender penis tube + sac that lacks a caecum (Fig. 4). The following key will distinguish these species. *Perlesta etnieri* is very similar and closely related to *P. nelsoni,* but the male can be distinguished by the darker pigmentation of the body and short distinct sensilla basiconica on tergum 10 (Fig. 2). The male of *P. nelsoni* is pale yellow and the sensilla basiconica are reduced (see Stark 1989, fig. 65). The long and slender paraprocts of *P. etnieri* with the apex curved posteriad and a mesoapical tooth (Fig. 3) are suggestive of *P. browni* Stark, a species known only from Arkansas and Oklahoma (Stark 1989, Poulton and Stewart 1991), and *P. cinctipes* (Banks) known from Illinois, Iowa, Kansas, Missouri, Nebraska and Oklahoma. The distinctive aedeagus of *P. etnieri* (Fig. 4) distinguishes it from the above species.

The egg of *P. etnieri* is similar to *P. cinctipes* (see Stark 1989, fig. 17), but in *P. etnieri* the chorion is covered with shallow irregular pits, but the collar is sessile. The egg of *P. nelsoni* has a smooth chorion and a short slender collar (Stark 1989). Additionally, the subgenital plate of *P. etnieri* has a small V-shaped notch (Fig. 5), whereas the subgenital plate of *P. nelsoni* has a deep U-shaped notch (see Stark 1989, fig. 68).

Other adult stoneflies collected at the type locality were *Allocapnia granulata* (Claassen), *A. rickeri* Frison, *A. tennessa* Ross and Ricker, *Isoperla* sp., *Acroneuria frisoni* Stark and Brown, *Perlinella ephyre*

(Newman), *Perlesta adena* Stark, and a single female of another species of *Perlesta.*

KEY TO SPECIES OF THE *PERLESTA NELSONI* SPECIES GROUP

MALES

1. Penis without caecum (Fig. 4) 2
– Penis with a caecum (Stark 1989, fig. 1) . . . . not keyed here (see Stark 1989, DeWalt et al. 2001)
2. T10 sensilla basiconica numerous, arranged in a pair of slightly elevated, circular patches (Stark 1989, figs. 51–52; Kirchner and Kondratieff 1997, fig. 2) 3
– T10 sensilla basonica sparse, not in two patches (Fig. 2) 4
3. Paraprocts with spine on anteroapical margin (Stark 1989, fig. 52) . . . . *P. frisoni*
– Paraprocts without spine on anteroapical margin (Kirchner and Kondratieff 1997, figs. 3 and 4) . . . . *P. teaysia*
4. Wing membrane, veins and body pale yellow . . . . *P. nelsoni*
– Wing membrane, veins and body dark brown to black . . . . *P. etnieri*

NEW TENNESSEE RECORDS

We report two new state records for Tennessee. *Perlesta lagoi* Stark, a widespread midwestern species (Stark 1989, DeWalt et al. 2001) is reported for the first time from the Cumberland Plateau region. This species is similar to, and can be confused with *P. decipiens* (Walsh). Additionally, *P. adena* Stark, previously known only from Ohio, was collected in abundance from several small streams of the Eastern Highland Rim of the Interior Plateau region of north central Tennessee. This same region has also yielded the rare and presumably imperiled perlodid stonefly *Hydroperla rickeri* (Stark) (Nelson 1996), and the rare leptophlebiid mayfly *Paraleptophlebia kirchneri* Kondratieff and Durfee (Wiersema and Long 2000).

Material examined.—*Perlesta lagoi*: Tennessee, Bledsoe Co., Sequatchie River at Ninemile (N35°41′30.0″ W85°05′00.0″), 12 May 2000, R. F. Kirchner and B. C. Kondratieff, 4 ♂, 2 ♀ (CSU); Cumberland Co., Daddys Creek at Big Lick, US-127 South of Crossville (N35°48′23.2″ W85°01′17.8″), 12 May 2000, R. F. Kirchner and B. C. Kondratieff, 1 ♂ (BPS).

Perlesta adena: Tennessee, Sumner Co., small stream to Little Trammel Creek, at Turners Station (N36°36′25.2″ W86°16′25.9″), 11 May 2000, R. Kirchner and B. Kondratieff, 15 ♂, 1 ♀, 12 nymphs (CSU, RFK); Trousdale Co., tributary to Rocky Creek, at Philippi Church (N36°23′21.9″ W86°15′18.6″), 5 miles W of Hartsville, 11 May 2000, R. Kirchner and B. Kondratieff, 63 ♂, 9 ♀, 15 nymphs (CSU, RFK, BPS); same location as Philippi Church, 25 May 1999, B. P. Stark, 11 ♂, 3 ♀, 2 nymphs (BPS); Williamson Co., Harpeth River at Millview, Arno Road (N35°52′41.0″ W86°47′27.1″), 11 May 2000, R. F. Kirchner and B. C. Kondratieff, 2 ♂ (CSU).

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We thank Bill P. Stark of Mississippi College for confirming the specific status of *P. etnieri* and providing verification of *P. adena* and *P. lagoi.*

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DESCRIPTIONS OF TWO NEW SPECIES OF *FULVIUS* STÅL (HETEROPTERA: MIRIDAE: CYLAPINAE) FROM BRAZIL, WITH BIOLOGICAL AND BIOGEOGRAPHIC NOTES ON THE GENUS

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Abstract.—Two new Brazilian species, ***Fulvius paranaensis*** from the state of Paraná and ***F. vicosensis*** from the state of Minas Gerais, are described. Male genitalia and photographs of both species are provided to assist in identification and notes on general biology and biogeography are given for the New World species of *Fulvius*.

Key Words: Heteroptera, Miridae, *Fulvius, paranaensis, vicosensis,* new species, Brazil, biology, biogeography

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The cylapine genus *Fulvius* Stål (1862) includes about 65 species worldwide (Carvalho and Costa 1994, Schuh 1995). Schuh (1976) discussed the phylogenetic position of *Fulvius* within Cylapinae, and Carvalho and Ferreira (1994) provided a key to the New World cylapine genera, including *Fulvius.* Carvalho and Costa (1994) revised the New World *Fulvius,* described 22 new species, and included an identification key to the 42 known species. Most authors have recognized the placement of *Fulvius* in the cylapine tribe Fulviini (e.g., Henry and Wheeler 1988, Carvalho and Ferreira 1994), but Schmitz and Štys (1973) argued to give the tribe subfamily status, an action rejected as premature by Schuh (1976). Schuh (1995) in his world catalog treated the tribe as a junior synonym of Cylapini, but more recently Gorczyca (2000), based on a cladistic analysis of the subfamily, recognized four tribes, including Fulviini. A complete list of references to the species of *Fulvius* can be found in Henry and Wheeler (1988), Carvalho and Costa (1994), Schuh (1995), and Gorczyca (2000).

In this paper, we describe the two new Brazilian species, *F. paranaensis* from Paraná and *F. vicosensis* from Minas Gerais, to provide names for an ongoing faunal study. Provided are illustrations of male genitalia and photographs of both species to assist in identification and notes on biology and biogeography of the New World species of *Fulvius.*

Fulvius Stål 1862

Fulvius Stål 1862: 322. Type species: *Fulvius anthocoroides* Stål. Monotypic.

Diagnosis.—*Fulvius* is recognized by the small to medium size, elongate body, length 1.4 to 5.5 mm; dark castaneous to brown general color, most species with whitish areas at middle of clavus and base of cuneus; long, produced head; eyes extending ventrally to gula, gula long; horizontal or nearly horizontal frons; long rostrum, extending to metacoxae or beyond; trapeziform pronotum, with rounded lateral margins and a sinuate posterior margin; large confluent calli, occupying anterior two-thirds; prominent collar; broadly exposed mesoscutum; macropterous subparallel hemelytra, with well-developed membrane and 2 closed cells; greatly reduced ostiolar opening, auricle, and evaporative area; long, slender legs; long metatibiae, much longer than pro- or mesotibiae; 2-segmented tarsi; and slender claws, usually with a subapical tooth.

BIOLOGICAL NOTES

While very little specific information is available on the biology, evidence suggests that members of the genus are largely predaceous and, possibly, mycetophagous. Large numbers of *Fulvius* often are attracted to lights (Carvalho 1956, Maldonado 1969, Schuh 1976, Paula and Ferreira 1998), including *F. vicosensis. Fulvius imbecilis* (Say) has been observed feeding on dipterous and coleopterous larvae and other soft-bodied arthropods found in damp areas or on fungi under loose bark of poplar (*Populus* sp.) firewood (Kelton 1985). *Fulvius quadristillatus* (Stål) has been associated with fungi (Auricularia) growing on decaying trees at the headwaters of the Rio Negro, Amazon, Brazil (Carvalho 1954), and has been taken in large numbers from litter and kitchen middens where fungi are abundant (Schuh 1976), but also where there is an abundance of larvae that might serve as prey. One Old World species has been reared through multiple generations on butterfly eggs and larvae (Gorczyca 2000). *Fulvius paranaensis* was found feeding on liquified material of dead vertebrate carcasses, a nutrient source perhaps not too dissimilar from that acquired from various arthropod prey.

BIOGEOGRAPHIC OVERVIEW

Members of the genus *Fulvius* are most abundant in tropical regions of the world, with approximately 92 percent of species distributed between the Tropics of Cancer and Capricorn. The majority of the species occur in the Neotropics. Prior to this study, Mexico had the largest number of species recorded (16 species), followed by Brazil (15 species) and Panama (13 species). Other countries range from 1 to 7 species. Fifty-eight percent of species are known from only one country, whereas 42 percent have been reported from two or more countries. The center of diversity for the New World species appears to be Mexico and possibly adjacent Central America, radiating northward into the United States and Canada and southward into Central and South America. *Fulvius anthocoroides* Stål has the largest range, occurring in 22 countries, followed by *F. bisbistillatus* (Stål) (17), *F. breddini* Reuter (12), *F. quadristillatus,* and *F. variegatus* Poppius (10). Insufficient collecting probably accounts for the limited distribution now known for many species. *Fulvius anthocoroides* is recorded from North America (United States [Florida only]), Central America (Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, and Panama), and South America (Bolivia, Brazil, Colombia, Ecuador [including Galapagos Islands], French Guiana, Guyana, Paraguay, Peru, Suriname, and Venezuela), extending into the Caribbean islands. The species *F. bisbistillatus, F. breddini,* and *F. quadristillatus* are also widely distributed, radiating from Mexico southward into South America. *Fulvius quadristillatus* also occurs in the Caribbean islands, and *F. breddini* is reported from the Galapagos islands. These last three mentioned species are sympatric with *F. anthocoroides* in almost all its distribution, except for North America. *Fulvius variegatus,* the species having the fourth largest geographic distribution, ranges in the Pacific region from Hawaii south throughout the Bismarck Archipelago (New Britain, New Guinea, New Ireland, and Samoa) and Micronesian Island groups (Kusiae, Palau, Ponape, Truck, Yap). With the addition of the two new species presented in this paper, Brazil becomes the most speciose country, having 17 spe-

Figs. 1–2. Photographs of *Fulvius paranaensis*, ♂. 1, Dorsal aspect. 2, Lateral aspect.

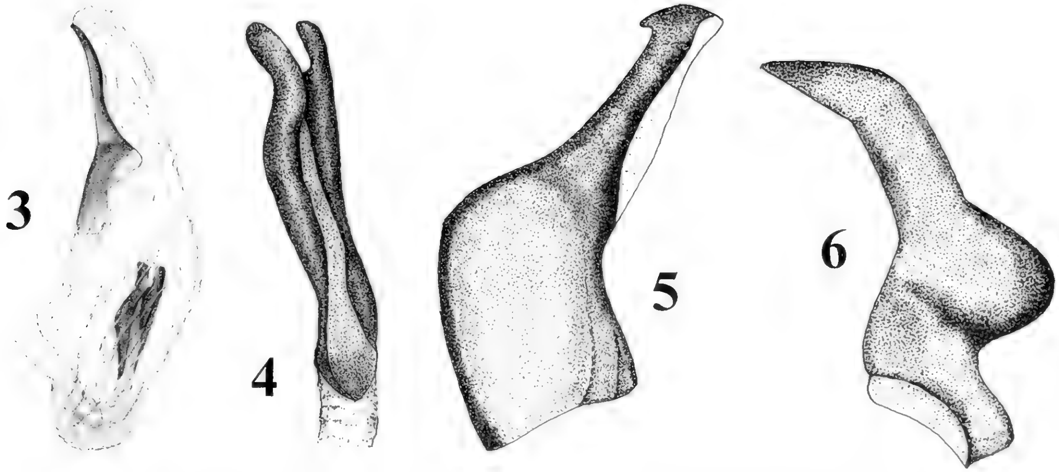
cies of *Fulvius*, and Minas Gerais, the most speciose Brazilian state, having seven species.

Fulvius paranaensis Ferreira and Henry, new species
(Figs. 1–6)

Diagnosis.—*Fulvius paranaensis* keys roughly to *F. gampoensis* Carvalho and Costa, but differs from it and other species of the genus in having the metacoxa brown only on basal ½ and pale apically (the mesocoxa is uniformly brown), antennal segment II narrowly pale on apical ⅕, and by the male genitalic characters, particularly the shape of elongate secondary gonopore (Fig. 4), the apically hooked phallotheca (Fig. 5), and the broad base of the left paramere (Fig. 6).

Description (Figs. 1–2).—Male (measurements include $\bar{x}$, followed by ranges in parentheses; n = 4): Length 4.31 mm (3.94–4.69 mm); width 1.25 mm (1.19–1.31 mm). *Head:* length 0.48 mm (0.52–0.45 mm); width 0.60 mm (0.60–0.62 mm); distance between eyes 0.29 mm (0.26–0.31 mm). *Antenna:* Segment I, length 0.48 mm (0.40–0.50 mm); II, 1.24 mm (1.16–1.33 mm); III, 0.50 mm (0.48–0.52 mm); IV, 0.71 mm (0.71 mm). *Pronotum:* Length 0.50 mm (0.48–0.50 mm); width 1.07 (1.10–1.05 mm). Length from cuneal fracture to apex of membrane 0.50 mm (0.48–0.50 mm); cuneal width 0.31 mm (0.26–0.33 mm).

General coloration dark brown with white and red areas. Head dark brown with apex of clypeus and outer margin of buccula red. Eye dark brown. Rostrum brown to fuscous, becoming darker apically, extending to middle of abdomen. Antenna fuscous, segment I reddish brown, segment II dark brown with apical ¼ white. Pronotum dark brown, collar with two fuscous spots; calli occupying ⅔ of disc; posterior margin of pronotum concave with posterior angles rounded. Mesoscutum brown with lateral margins red. Scutellum brown. Hemelytron brown; irregular yellow band on base of corium extending to embolium and apex of clavus; base of cuneus white, apex dark brown; apical area of embolium near



Figs. 3–6. Male genitalia of *Fulvius paranaensis*. 3, Vesica. 4, Secondary gonopore. 5, Phallotheca. 6, Left paramere.

cuneus, red; membrane fuscous, iridescent, with a small pale area near inner margin of cuneus. Ventral region dark brown. Pro- and mesolegs pale brown except coxae dark brown; metaleg with apical ½ of coxa and trochanter whitish; setae short, erect or semierect. Head, xyphus, pronotum, propleura, mesoscutum, and scutellum shagreened, almost glabrous, except for very short setae on apical area of head. Antennal segments I and II with short erect or semierect setae ranging from shorter than, to as long as, diameter of segments; setae on segments III and IV longer than diameters of their respective segments; segment II slightly incrassate toward apex; relative lengths of antennal segments in ascending order I < III < IV < II. Male genitalia: Vesica (Fig. 3) without lobe or fields of spines and spicules. Secondary gonopore long (Fig. 4), with a lobe on each side. Phallotheca reduced (Fig. 5), membranous, apex acuminate, posterior region enlarged. Right paramere very small and simple. Left paramere (Fig. 6) distally acute, with median lobe glabrous.

Female (n = 3).— Length 4.69 mm (4.69 mm); width 1.54 mm (1.50–1.56 mm). *Head:* Length 0.55 mm (0.50–0.60 mm); width 0.66 mm (0.64–0.67 mm); distance between eyes 0.32 mm (0.31–0.33 mm). *Antenna:* Segment I length, 0.49 mm (0.48–0.50 mm); II, 1.06 mm (1.02–1.10 mm); III, 0.48 mm (0.48 mm); IV, 0.69 mm (0.62–0.74 mm). *Pronotum:* Length 0.60 mm (0.60 mm); width 1.27 mm (1.24–1.31 mm). Length from cuneal fracture to apex of membrane 0.49 mm (0.48–0.50 mm); cuneal width 0.32 mm (0.29–0.33 mm).

Similar to male in color, structure, and vestiture.

Type specimens.—Holotype ♂, Curitiba, PR, 30/I/94, M.O. Moura (Museu Nacional, Rio de Janeiro). Paratypes: Same locality as for holotype, with following dates: 3 ♂: 12/XI/1993, 30/I/1994, 20/I/1994; 3 ♀: 19/I/1994, 30/I/1994 and 27/I/1994 (all in Museu Nacional and Universidade Federal de Viçosa, MG, Brazil, except 1 ♂, 1 ♀ in National Museum of Natural History, Washington, DC).

Etymology.—Named for the state of Paraná, Brazil, in which this species occurs.

Distribution.—Curitiba, Paraná, Brazil.

Discussion.—According to Mr. Mauricio Moura (personal communication), the specimens were collected in a secondary forest at the Botanical Garden of Curitiba, feeding on the exudates of a dead animal in an advanced state of decomposition.

Figs. 7–8. Photographs of *Fulvius vicosensis*, ♀. 7, Dorsal aspect. 8, Lateral aspect.

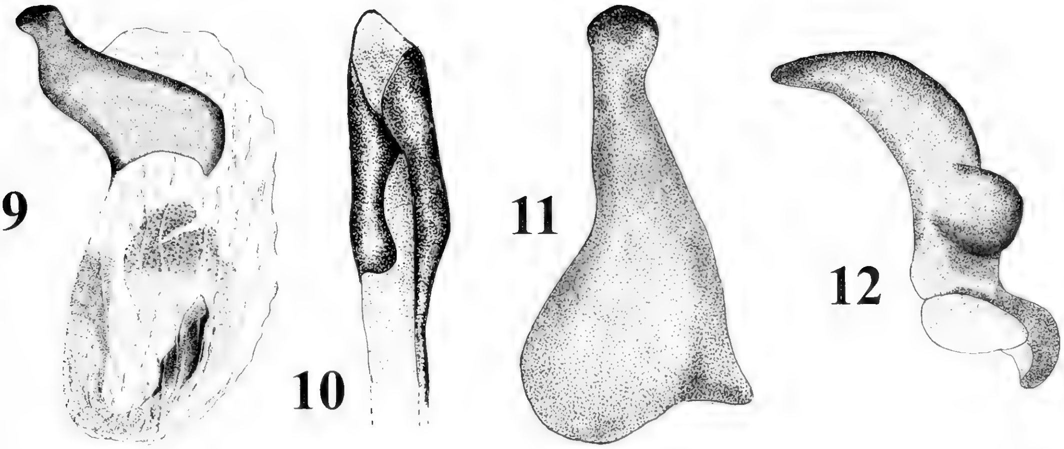
Fulvius vicosensis Ferreira and Henry, new species

(Figs. 7–12)

Diagnosis.—*Fulvius vicosensis* keys to *F. bisbistillatus* (Stål) in Carvalho and Costa (1994), but can be distinguished by the proportionately shorter second antennal segment having the apical ⅖ white and the broader basal width of the pronotum. It also can be distinguished from all other species of the genus by the male genitalia, particularly the more elongate trough of the secondary gonopore (Fig. 10), the absence of an apical notch on the phallotheca (Fig. 11), and the more bulbous base on the left paramere (Fig. 12).

Description.—Male (measurements include $\bar{x}$, followed by ranges in parentheses; n = 10): Length 3.53 mm (3.25–4.06 mm); width 1.17 mm (0.94–1.38 mm). *Head:* Length 0.43 mm (0.33–0.52 mm); width 0.55 mm (0.52–0.61mm); distance between eyes 0.19 mm (0.17–0.21 mm). *Antenna:* Segment I length 0.43 mm (0.33–0.48 mm); II, 0.95 mm (0.88–1.07 mm); III, 0.49 mm (0.47–0.59 mm); IV, 0.62 mm (0.57–0.69 mm). *Pronotum:* Length 0.39 mm (0.33–0.47 mm); width 1.27 mm (1.24–1.31 mm). Length from cuneal fracture to apex of membrane 0.36 mm (0.33–0.48 mm); cuneal width, 0.23 mm (0.21–0.29 mm).

General color brown with white areas. Head dark brown with apex of clypeus pale; rostrum pale brown, becoming fuscous apically; antennal segment I brown with apex paler; segment II with apical ⅓ white, other segments dark brown. Eye dark brown. Pronotum and collar dark brown. Mesonotum dark brown with lateral margins paler. Scutellum dark brown. Hemelytron dark brown with an irregular stripe extending through apex of clavus, basal area on corium and embolium yellow; base of cuneus white. Membrane darkened, slightly iridescent, area near inner margin of cuneus pale. Legs pale brown with coxae and trochanters pale; setae short, erect or semierect. Underside of body brown. Head, pronotum, propleuron, mesoscutum, and scutellum glabrous [or rubbed], except for short setae on apical area of head. Rostrum extending beyond metacoxae. Antennal segment I and II



Figs. 9–12. Male genitalia of *Fulvius vicosensis*. 9, Vesica. 10, Secondary gonopore. 11, Phallotheca. 12, Left paramere.

with erect or semierect setae ranging from shorter than to as long as diameter of segments; setae on segments III and IV longer than diameters of their respective segments; antennal segment I longer than width between eyes; antennal segment II slightly incrassate toward apex, III and IV thinner; relative lengths of antennal segments in ascending order I < III < IV < II. Posterior margin of pronotum concave with posterior angles rounded; collar well defined; calli occupying anterior ⅔ of pronotum. Hemelytron with short reclining setae. Ventral region of thorax glabrous (or rubbed); abdomen with short to relatively long simple setae. Male genitalia: Vesica (Fig. 9) with two fields of short spines near the secondary gonopore. Secondary gonopore (Fig. 10) short, apex acute. Phallotheca (Fig. 11) small, membranous, apical half acuminate with apex enlarged and rounded. Right paramere small, simple. Left paramere (Fig. 12) falciform, median lobe glabrous.

Female (Figs. 7, 8) (measurements include $\bar{x}$, followed by ranges in parentheses; n = 10).—Length 3.67 mm (3.81–3.84 mm); width 1.13 mm (1.00–1.19). *Head:* Length 0.45 mm (0.38–0.50 mm); width 0.57 mm (0.52–0.60 mm); distance between eyes 0.20 mm (0.19–0.21 mm). *Antenna:* Segment I length 0.42 mm (0.36–0.48 mm); II, 0.77 mm (0.76–0.98 mm); III, 0.53 mm (0.50–0.55 mm); IV, 0.71 mm (0.71 mm). *Pronotum:* Length 0.43 mm (0.40–0.45 mm); width 1.01 mm (0.93–1.05 mm). Length from cuneal fracture to apex of membrane 0.39 mm (0.36–0.45 mm); cuneal width, 0.23 mm (0.21–0.26 mm).

Similar to male in color, structure, and vestiture.

Type specimens.—Holotype ♂, Viçosa, Minas Gerais, Brasil, Armadilha Luminosa, Córrego do Paraíso, 17/03/1988, P. S. F. Fiuza (Museu Nacional, Rio de Janeiro) Paratypes: Same locality as for holotype, with following dates: 16 ♂: 23/II/1988, 09/XII/1982, 02/II/1986, 19/I/1983, 08/I/1988, 14/I/1993, 18/II/1983, 11/III/1983, 10/XII/1986, 01/VI/1983, 17/VI/82, 08/I/1988, 02/II/1983, 22/XII/1982, 05/III/1987; 17 ♀: 20/I/1982, 25/II/1982, 31/III/1987, 11/III/1987, 13/I/1987, 18/I/1988, 08/II/1993, 08/I/1988, 23/II/1988, 25/II/1986, 02/II/1983, 10/IV/1987, 23/VI/1982, 20/IV/1983, 12/II/1979, 24/II/1983 (all paratypes in Museu Nacional and Universidade Federal de Viçosa, MG, Brazil, except for 3 ♀ in National Museum of Natural History, Washington, DC).

Etymology.—Named for the city of Viçosa, Brazil, in which this species occurs.

Distribution.—Viçosa, Minas Gerais, Brazil.

Discussion.—The paratypes compare well with the holotype, varying in general color from paler to slightly darker. The specimens were collected in black light traps in a secondary forest at Viçosa known as "Mata do Córrego do Paraiso (20°46′–20°48′S; 45°50′–45°52′W)," characterized by Atlantic Forest vegetation, at an altitude of 600–700 meters, an annual average temperature of 18° C to 19° C, and an annual average precipitation of about 131.5 cm.

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A REVIEW OF THE NEW RIODINID BUTTERFLY GENUS *PANAROPSIS* (LEPIDOPTERA: RIODINIDAE: SYMMACHIINI)

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Abstract.—A new riodinid genus ***Panaropsis,*** tribe Symmachiini, is described and illustrated from Central and South America. Four species are recognized: *elegans* Schaus and *semiota* Bates transferred from *Pterographium* Stichel (**n. comb.**), and *thyatira* Hewitson and *inaria* Westwood transferred from *Esthemopsis* C. and R. Felder (**n. comb.**).

Key Words: *Esthemopsis,* Neotropical, *Pterographium, Panaropsis,* Symmachiini

The purpose of this paper is to describe and characterize a new riodinid genus in the tribe Symmachiini to provide a generic name for *elegans* Schaus 1920, *semiota* Bates 1868, *inaria* Westwood [1851] and *thyatira* Hewitson [1853], currently treated in *Pterographium* Stichel 1910 and *Esthemopsis* C. and R. Felder 1865, for a forthcoming morphological survey of male androconia in the Riodinidae (Hall and Harvey, in press). The tribe Symmachiini has been adequately diagnosed elsewhere (Harvey 1987, Hall and Willmott 1996) and this information is not repeated here.

METHODS

Dissections were made using standard techniques, after abdomens were soaked in hot 10% potassium hydroxide solution for approximately five minutes, and subsequently stored in glycerol. The terminology for male and female genital and abdominal structures follows Klots (1956) and Eliot (1973), while nomenclature for wing venation follows Comstock and Needham (1918). The taxonomic status of names is based on the catalog of Callaghan and Lamas (in press).

All the collections listed by Hall (1999) were examined to determine the ranges of *Panaropsis* species. The following collection acronyms are used throughout the text: AME: Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, U.S.A.; BMNH: The Natural History Museum, London, England; MNRJ: Museu Nacional, Rio de Janeiro, Brazil; MUNB: Museo de la Universidad Nacional, Bogotá, Colombia; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; ZMHU: Zoologisches Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

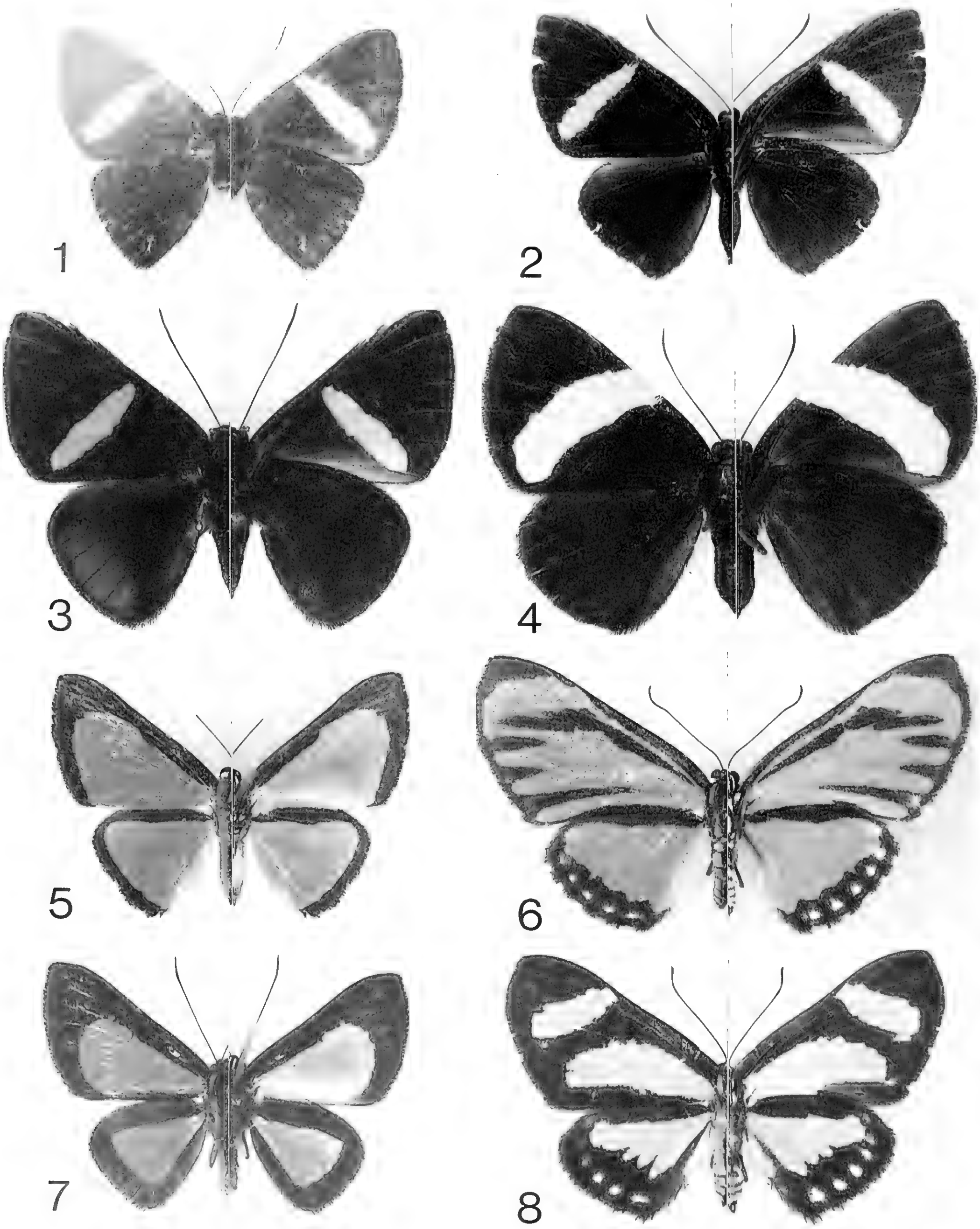
SYSTEMATICS

Panaropsis Hall, new genus
(Figs. 1–8, 9, 10–14, 15–17, 18)

Type species.—*Panara elegans* Schaus 1920.

Etymology.—The name alludes to the superficial similarity between members of the riodinine genus *Panara* and the type species *elegans,* which was formerly placed in *Panara.*

Description.—*Male:* Forewing length 17–20 mm. *Wing shape:* both wings typically somewhat elongate; forewing costa very slightly arched at base, distal margin



Figs. 1–8. Adults (dorsal surface on left, ventral surface on right). 1, *Pterographium sicora,* male, Brazil, Espírito Santo, Linhares [AME]. 2, *Panaropsis semiota,* male, French Guiana, Cayenne, Galion [USNM]. 3, *P. elegans,* male, Panama, Panamá, nr. El Llano [USNM]. 4, *P. elegans,* female, Panama, Colón, Colón [USNM]. 5, *P. thyatira,* male, Brazil, Mato Grosso, Diamantino [USNM]. 6, *P. thyatira,* female, Brazil, Mato Grosso, Colegio Buriti [USNM]. 7, *P. inaria,* male, Brazil, Pernambuco, São Lourenço [USNM]. 8, *P. inaria,* female, Brazil, Pernambuco, São Lourenço [USNM].

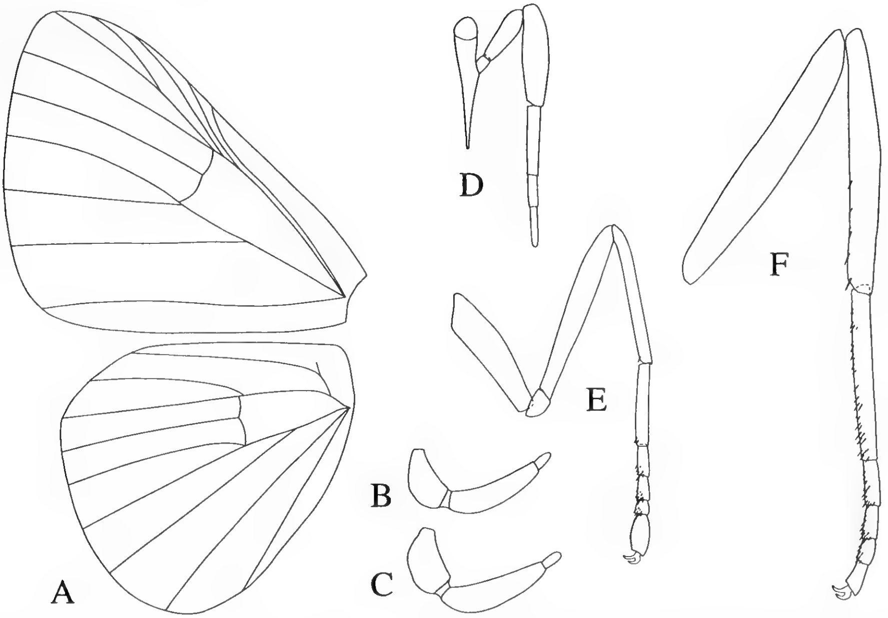


Fig. 9. Morphology of *Panaropsis elegans*. A, Male venation. B, Male palpus. C, Female palpus. D, Male foreleg. E, Female foreleg. F, Male hindleg.

slightly convex; hindwing slightly pointed at apex and tornus. *Venation* (Fig. 9A): four forewing radial veins. *Dorsal surface:* ground color of both wings black; forewing with a diagonal yellow or red postdiscal band and hindwing black or with iridescent blue patch (*semiota* and *elegans*) or both wings with a large orange patch (*thyatira* and *inaria*); patch of erectile androconial setae at base of hindwing cell Cu2, dense in *semiota* and *elegans,* diffuse in *thyatira* and *inaria*; fringe on both wings black. *Ventral surface:* same as dorsal surface but paler and with no iridescence. *Head:* labial palpus entirely black (*semiota* and *elegans*) or with white scaling ventrally (*thyatira* and *inaria*), second and third segments short (Fig. 9B); eye brown and bare, black or white scaling at margins; frons black with white lateral scaling dorsally in *thyatira* and *inaria*; antennal length approximately 70% of forewing length, segments black without white scaling at base; club long and black, tips often orange brown. *Body:* thorax and abdomen broad and robust; dorsal and ventral surface of thorax and abdomen black in *semiota* and *elegans,* tegula black with variably prominent red anterior spot in *elegans*; dorsal surface of thorax black with orange tegula and orange lateral scaling, ventral surface black with patches of white scaling in *thyatira* and *inaria,* dorsal surface of abdomen black with remainder orange in *thyatira* and *inaria,* also black scaling ventrally in *inaria*; a narrowly medially divided band of concealed androconial scales on dorsal half of anterior margin of abdominal tergites four and five; tarsus of foreleg trimerous, coxa of medium length for family (Fig. 9D); legs black, midleg and hindleg with a tibial spur, a scattered group of spines along distal inner margin of tibia and two dense rows of spines along distal inner margin of tarsal segments (Fig. 9F). *Genitalia* (Figs. 10–14): overall large; uncus rectangular and produced into small medial point dorsally, falces and tegumen of average size and shape for family; vinculum evenly narrow with medium-sized rounded saccus ventrally; aedeagus short and very broad, everted vesica contains a straight row of approximately ten large anteriorly directed spines ventrally that become gradually shorter posteriorly, a large patch of large anteriorly directed spines dorsally that is slightly ventrally curved anteriorly and a sparse lateral patch of very small spines; pedicel short, narrow and strap-like; valvae curl ventrally and slightly overlap, upper portion rectangular, lower portion produced into one or two small rounded projections, setae on valvae typically only on upper rectangular portion and small raised ridge at middle.

Female: Differs externally from male in following ways: forewing length 19–25 mm. Both wings more rounded (and elongate in *thyatira* and *inaria*); ground color of both wings paler; *semiota* and *elegans* not significantly sexually dimorphic, females with no dorsal blue iridescence, broader forewing orange bands and white fringe elements on hindwing and in forewing apex; *thyatira* and *inaria* strongly sexually dimorphic, females with yellow or orange pattern elements divided into subapical and basal areas on forewing, white submarginal hindwing spots present, prominent white hindwing fringe elements present in *thyatira,* some lateral black scaling present on each abdominal segment. *Head:* second segment of labial palpus slightly broader (Fig. 9C). *Body:* foreleg with spines at inner distal tip of tibia and tarsal segments one to four, large ovoid patch of sensilla on swollen last tarsal segment (Fig. 9E). *Genitalia* (Figs. 15–17): corpus bursae elongate and slightly medially constricted, no signa present; ductus bursae short, broad and somewhat sclerotized with tiny spines lining inner surface, becoming suddenly broader and less sclerotized anterior to broad opening of ostium bursae which is positioned in desclerotized invagination between eighth and seventh abdominal sternites; eighth sternite sclerotized and slightly concave medially.

Diagnosis.—Having examined the internal male abdominal morphology of approximately 95% of species in the tribe Symmachiini (males are not known for several of the remainder) for a paper surveying male androconia in the Riodinidae (Hall and Harvey, in press), it became clear that four species which were currently treated in *Pterographium* (*semiota* and *elegans*) and *Esthemopsis* (*thyatira* and *inaria*) were more closely related to each other than to any other symmachiine species. These four species, which I place in the new genus *Panaropsis,* present a rather heterogeneous external appearance, but their morphology is very homogeneous. The only external similarities are their relatively large size for riodinds, somewhat elongate wing shapes and robust thoraces and abdomens, whereas the only interspecific genital variation lies in differences in the shapes of the valvae and dorsal cornutal band in males. There are two unique male genital synapomorphies for *Panaropsis.* One is the arrangement of the aedeagal cornuti, with a straight row of large spines ventrally, a scattered patch of very small spines laterally and an anteriorly recurved dense band of large spines dorsally. The other is the shape of the valvae, which are curled ventrally to partially overlap and posses a lower portion produced into one or two small "finger-like" projections.

Systematic position.—Although two *Panaropsis* species, *semiota* and *elegans,* externally closely resemble the sole member of *Pterographium, sicora,* the male genitalia differ substantially in almost every respect (see Figs. 10–12), suggesting that the two genera may not be closely related. Given the prevalence of aposematic and putatively mimetic coloration in the tribe, such wing pattern convergence would not be surprising. It is presently not certain what the closest relatives of *Panaropsis* are. Only a few *Symmachia* Hübner [1819] species, all *Stichelia* Zikán 1949, one *Mesene* Doubleday 1847, two *Xenandra* C. and R. Felder 1865, and one *Esthemopsis* possess medially divided concealed abdominal androconia on segments four and five as in *Panaropsis,* but none of these taxa closely resemble *Panaropsis* species in external appearance or morphology. I tentatively place *Panaropsis* near *Pterographium* and *Pirascca* Hall and Willmott 1996, based on the presence in males of dense erectile androconial setae at the anal margin of the dorsal hindwing (also found in several unrelated *Symmachia* species) and similarities in the ultrastructure of the concealed male abdominal androconial scales (the ultrastructure of these scales has been examined for representatives from each symmachiine genus using scanning electron microscopy), which are elongate, narrow and apically curved in all three genera (see Fig. 18; also illustration in Hall and Willmott (1996) for *Pirascca*). Those of *Pterographium* and *Pirascca* are particularly similar to each other.

Proposed classification.—Below is presented a synonymic checklist for *Panaropsis.*

Panaropsis Hall, n. gen.

elegans (Schaus, 1920), **n. comb.**
  = *chocoensis* (Callaghan, 1999), **n. syn.**
inaria (Westwood, [1851]), **n. comb.**
  = *barca* (Hewitson, [1853])
semiota (Bates, 1868), **n. comb.**
  = *similatum* (Zikán, 1949)
thyatira (Hewitson, [1853]), **n. comb.**
  = *isabellae* (Sharpe, 1890)
  = *perfluxa* (Stichel, 1924)
  = *phlegontis* (Stichel, 1910)
  = *sarta* (Stichel, 1924)

Biology.—*Panaropsis* species are uncommon to rare inhabitants of wet lowland forests below 1000 m, and little is known of their biology. Males are typically encountered perching in hilltop forest lightgaps, often very high above the ground, and their flight is rapid. Both sexes of *P. elegans* have been recorded nectaring on *Terminalia* and *Croton* flowers (DeVries 1997). All species are brightly and aposematically colored and resemble a number of distasteful moths in the families Arctiidae and Notodontidae.

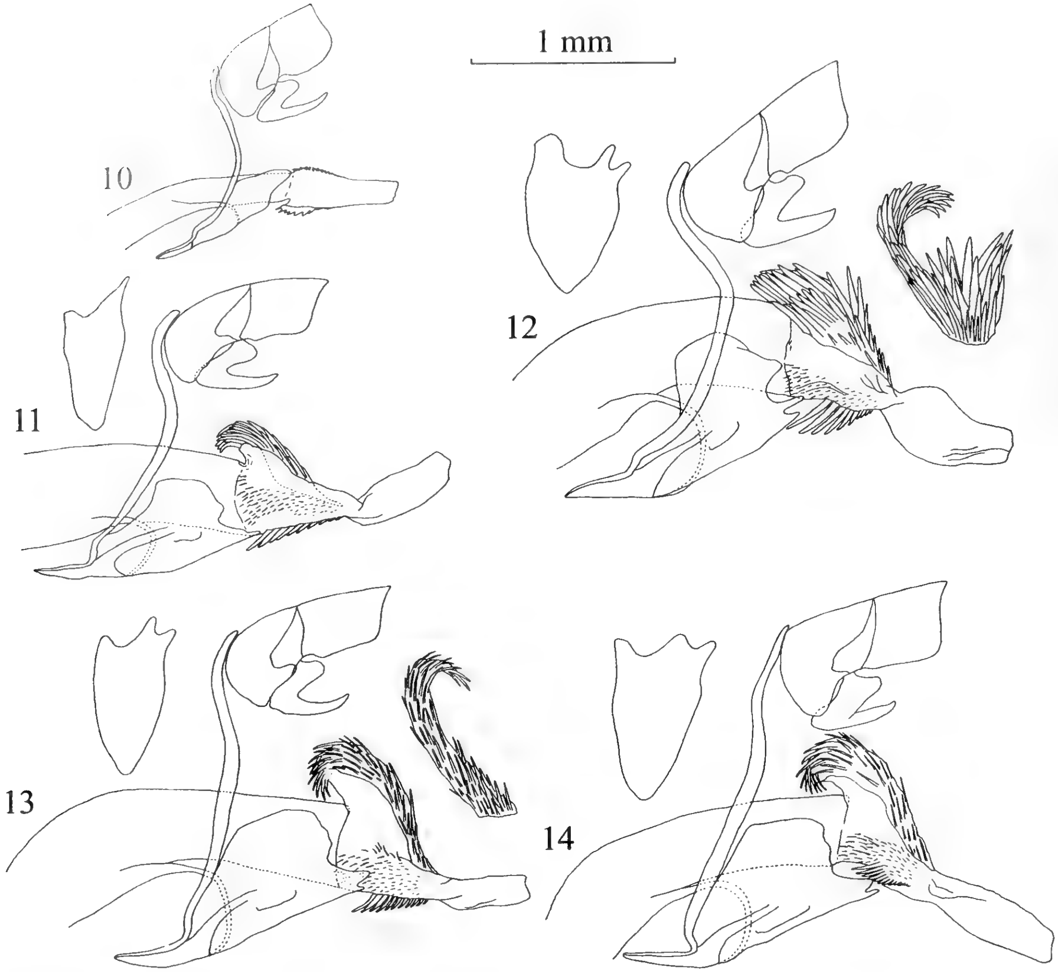
Distribution.—*Panaropsis* is a pan-Neotropical genus whose species occur from Mexico to western Ecuador, throughout the Guianas and Amazon basin, and into southeastern Brazil.

Panaropsis semiota (Bates 1868), **n. comb.**
(Figs. 2, 11)

Limnas semiota Bates 1868: 380–381. Type locality: Alter do Chão, Rio Tapajós, E. Brazil. Syntype male BMNH [examined].
Pterographium similatum Zikán 1949: 536–538, figs. 1–3. Type locality: São Gabriel, Rio Negro, N. Brazil. Holotype male and allotype female MNRJ [type illustrations examined].

Identification and taxonomy.—Typical FW length: male 17 mm; female 18 mm (Zikán 1949). The taxon *semiota* was long treated in the riodinine genus *Melanis* Hübner [1819] (Stichel 1910, 1930–31; Bridges 1994), but was transferred, along with the newly synonymized *similatum,* to the monotypic *Pterographium* by Hall and Willmott (1996), on the basis of external similarities with the type species of that genus, *sicora. Panaropsis semiota* differs externally from the southeastern Brazilian *Pterographium sicora* only by lacking prominent blue dorsal iridescence and orange scaling at the tip of the abdomen, and by possessing a more robust thorax and abdomen. However, despite the remarkable external similarities, the male genitalia are completely distinct (see Figs. 10 and 11). *Panaropsis semiota* differs from its sister species *P. elegans* by its smaller size, more elongate wing shape and more distally positioned postdiscal forewing band, by lacking an iridescent blue patch on the dorsal hindwing, and in the male genitalia by having a slightly shallower indented notch between the upper and lower portions of the valvae, a lower valve portion with one instead of two small projections and slightly smaller cornutal spines.

Biology.—This very rare species is only known from a handful of specimens in col-



Figs. 10–14. Male genitalia. 10, *Pterographium sicora*. 11, *Panaropsis semiota*. 12, *P. elegans*. 13, *P. thyatira*. 14, *P. inaria*.

lections. Brévignon and Gallard (1998) report finding males in French Guiana perching on forested hilltops between 1330 and 1430 h on top of leaves 3 to 4 m above the ground; their flight is rapid.

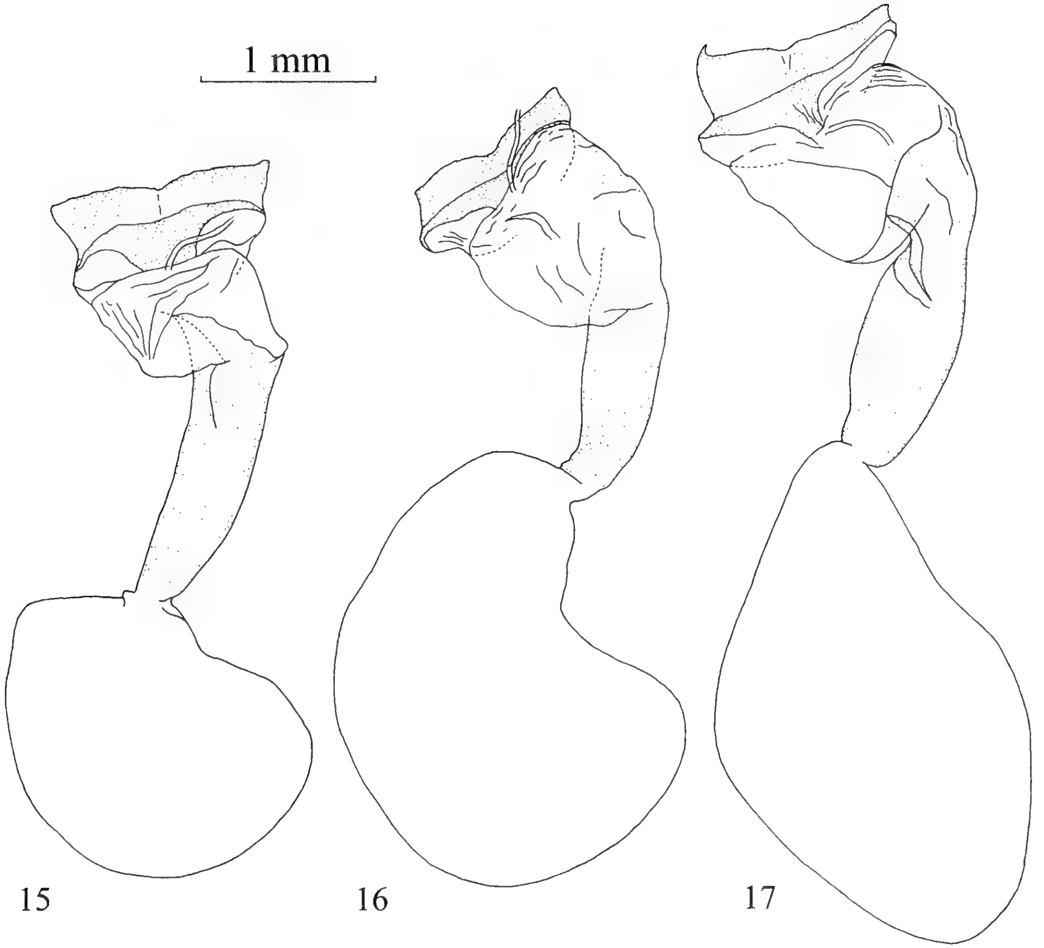
Distribution.—Brazil (central and lower Amazon) and French Guiana.

Panaropsis elegans (Schaus 1920), **n. comb.**
(Figs. 3–4, 9, 12, 15)

Panara elegans Schaus 1920: 108. Type locality: Cayuga, Guatemala. Syntype males (7) and females (5) USNM [examined].

Pterographium elegans chocoensis Callaghan 1999: 1053, 1055, figs. 25–28. Type locality: Aguas Claras, Río Anchicayá, W. Colombia. Holotype male MUNB [type illustrations examined]. **n. syn.**

Identification and taxonomy.—Typical FW length: male 18 mm; female 21 mm. The taxon *elegans* was described (Schaus 1920) and subsequently treated (Stichel 1910, 1930–31; Bridges 1994) in the genus *Panara* Doubleday 1847, in the tribe Riodinini. Harvey (1987) discovered that males of *elegans* possessed concealed abdominal androconia, placing it in the tribe Symma-



Figs. 15–17. Female genitalia in dorsal view. 15, *Panaropsis elegans*. 16, *P. thyatira*. 17, *P. inaria*.

chiini, but he did not transfer it to any other genus. Callaghan (1997) transferred *elegans* from *Panara* to the symmachiine genus *Pterographium* on the basis of it sharing "erectile scent hairs in cell Cu2-2A of the dorsal hindwing" with the type species of that genus. However, certain members of *Symmachia* and *Pirascca* also possess such hair tufts, and the fact that some members of *Panaropsis* possess such clearly defined hair tufts while others do not (*thyatira* and *inaria*) indicates this structure is homoplasious even at the species-group level, and thus not a reliable generic character.

Both sexes of *P. elegans* possess common riodinid wing patterns. Within the Symmachiini, males somewhat resemble *Esthemopsis pherephatte* (Godart [1824]) and *Pterographium sicora* (Hewitson 1875), but their large size, rounded wing shape and prominent iridescent dorsal hindwing blue patch are distinctive. The female of *P. elegans* resembles those of many species in genera such as *Hypophylla* Boisduval 1836, *Panara, Pirascca, Setabis* Westwood [1851] and *Symmachia*, but its large size, entirely brown ventral surface and largely white hindwing fringe are diagnostic.

Panaropsis elegans varies slightly geographically. Males from Mexico to Costa Rica typically have dorsal hindwing blue restricted to an ovoid patch in the distal third of the wing and a forewing orange band that extends to the tornus, whereas in males from Costa Rica eastwards the blue tends to extend more proximally to the discal cell and the forewing orange band does not reach the tornus. The width of the forewing band and its color, which varies from orange to red, and the prominence of red scaling at the anterior tip of the tegula is variable throughout the range of the species. Callaghan (1999) described the subspecies *chocoensis* from a small series of males and females from a single locality in western Colombia on the basis of the male forewing band being red instead of orange. However, since red-banded males occur rarely throughout the range of *P. elegans* (e.g., see the illustrations in d'Abrera (1994) and DeVries (1997) of specimens from Nicaragua and Costa Rica respectively), I synonymize *chocoensis* with *elegans*.

Biology.—*Panaropsis elegans* is an uncommon inhabitant of lowland rainforest from sea-level to 900 m. DeVries (1997) reports finding males in Costa Rica as solitary individuals or in small groups perching along forest edges, trails, streams and in shaded forest light gaps; individuals perched between 2 and 5 m above the ground under leaves from 0800 to 1230 h and their flight was fast and erratic. Callaghan (1999) reports finding males in Colombia perching on hilltops from 1000 to 1200 h under leaves with wings outspread 2 to 3 m above the ground. Both sexes visit flowers of *Terminalia* and *Croton* (DeVries 1997).

Distribution.—Mexico to western Ecuador.

Panaropsis thyatira (Hewitson [1853]), **n. comb**

(Figs. 5–6, 13, 16)

Limnas thyatira Hewitson [1853]: pl. 59, fig. 6. Type locality: "Amazon". Syntype female BMNH [examined].

Lymnas isabellae Sharpe 1890: 571, pl. 46, fig. 3. Type locality: Rio Araguaia, S. Brazil. Syntype male BMNH [examined].

Lymnas thyatira phlegontis Stichel 1910: 205. Type locality: Río Songo, Bolivia. Holotype female ZMHU [examined].

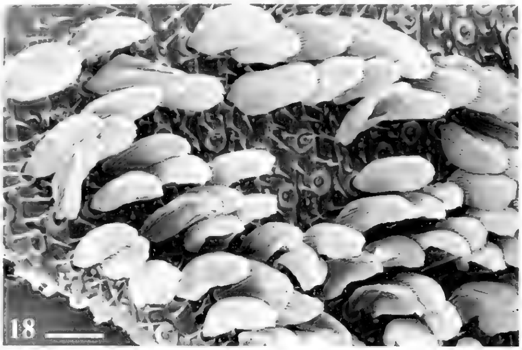


Fig. 18. Scanning electron micrograph of concealed male abdominal androconial scales. Scale bar = 20 μm.

Limnas inaria thyatira f. *perfluxa* Stichel 1924: 2. Type locality: Santarém, E. Brazil. Holotype male ZMHU [examined].

Limnas inaria thyatira f. *sarta* Stichel 1924: 2. Type locality: Santarém, E. Brazil. Holotype female ZMHU [examined].

Identification and taxonomy.—Typical FW length: male 17 mm, female 22 mm. The taxon *thyatira* was described (Hewitson 1852–54) and long treated as a species in *Limnas* Boisduval 1836 (now a synonym of *Melanis*), and transferred to *Esthemopsis* as a subspecies of *inaria* by Stichel (1924). It has subsequently remained in *Esthemopsis* and been treated variably as a subspecies of *inaria* (Bridges 1994) or as a full species (d'Abrera 1994; Callaghan and Lamas, in press). I follow Callaghan and Lamas (in press) in regarding *thyatira* as a species distinct from *inaria* because of the substantial differences in the wing pattern and shape of the females and the fact that each species occupies a distinct biogeographic zone (i.e., the Amazon basin and southeastern Brazil).

The male of *P. thyatira* differs from that of *P. inaria* by having orange on the hindwing that extends to the anal margin and predominantly orange instead of black scaling ventrally on the abdomen. The female has a broader wing shape, with orange instead of yellow patterning that forms rays on the forewing. The male and female genitalia of both species do not differ. The male genitalia of *thyatira* and *inaria* differ from those of *semiota* and *elegans* only by having a dorsal cornutal patch that contains narrower spines and is restricted to a narrow band on the left-hand side without the additional contiguous posterior patch on the right-hand side (see Figs. 12 and 13).

Both sexes exhibit some wing pattern variation, which has led to the description of several unwarranted subspecific and infrasubspecific names. In both sexes, the extent of distal orange on both wings is variable, and in males a black interneural line in cell Cu2, as in the female, and submarginal white spots on the ventral hindwing may be present or absent.

Biology.—Brévignon and Gallard (1998) report finding males of this uncommon species in French Guiana perching on hilltops between 1530 and 1645 h on top of leaves 5 m above the ground. In Ecuador, males were similarly encountered singly or in small groups perching on a forested hilltop 10 to 15 m above the ground on top of sunlit leaves with their wings outspread (Hall and Willmott, unpubl. data). Notably, the female resembles a number of nymphalid heliconiine species, such as *Dryas julia* (Fabricius 1775), *Eueides lineata* Salvin 1868 and *Eueides aliphera* (Godart 1819).

Distribution.—Colombia to Bolivia, Brazil (Amazon and southern Brazil) and the Guianas.

Panaropsis inaria (Westwood [1851]), **n. comb.**

(Figs. 7–8, 14, 17)

Limnas inaria Westwood [1851]: 460, pl. 73, fig. 7. Type locality: "Brazil". Syntype male BMNH [examined].

Limnas barca Hewitson [1853]: pl. 60, fig. 12. Type locality: Rio de Janeiro, S.E. Brazil. Syntype female BMNH [examined].

Identification and taxonomy.—Typical FW length: male 17 mm, female 21 mm. The taxon *inaria* was also described (Westwood 1850–52) and long treated as a species in *Limnas* and transferred to *Esthemopsis* by Stichel (1910). *Panaropsis inaria* is distinguished from its sister species, *P. thyatira,* in the previous species account. Note that the substantial sexual dimorphism in both these species led to the description of each sex as separate species. *Panaropsis inaria* and *P. thyatira* externally most closely resemble *Machaya obstinata* Hall and Willmott 1995, from the Andes of eastern Ecuador, but that species has reduced orange on both wings, an entirely black ventral hindwing and a black thorax and abdomen.

Biology.—Nothing is known about the biology of this uncommon species.

Distribution.—Southeastern Brazil (Rio de Janeiro to Pernambuco).

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NOTES ON THE RESPONSES OF HOST-SEEKING NYMPHS AND ADULTS OF THE TICKS *IXODES SCAPULARIS* AND *AMBLYOMMA AMERICANUM* (ACARI: IXODIDAE) TO CANINE, AVIAN, AND DEER-PRODUCED SUBSTANCES

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Abstract.—In laboratory and behavioral bioassays, host-seeking nymphs and adults of the blacklegged tick, *Ixodes scapularis* Say, were exposed to substances rubbed from the coats of dogs, from chicken feathers and from the interdigital glands of white-tailed deer, *Odocoileus virginianus* (Zimmermann). Nymphs of the lone star tick, *Amblyomma americanum* (L.) were exposed to substances from chicken feathers. Nymphs of *I. scapularis* became akinetic on surfaces rubbed with substances from chicken feathers, but *A. americanum* nymphs did not. Overall, nymphs of *I. scapularis* appeared to avoid substances rubbed from the coats of dogs. Although hair samples were obtained from 14 dogs maintained under the same conditions, substances from the hair of one dog elicited arrestant responses among nymphs and substances from the hair of another dog appeared to completely repel *I. scapularis* nymphs. Adult *I. scapularis* of both sexes showed high levels of arrestment when exposed to substances from the same canine hair samples. No arrestment was observed when *I. scapularis* nymphs were exposed to interdigital gland substances of white-tailed deer does.

Key Words: kairomones, blacklegged ticks, lone star tick

The host-finding behavior of ixodid (hard) ticks can be divided into two general types, ambushing and hunting (Waladde and Rice 1982). Typically, an ambushing tick waits on or near a vantage point, such as a twig or blade of grass, until a suitable host brushes against the tick's outstretched legs and it catches hold. Ticks that are considered hunters also spend much time waiting for a host, but when they detect the presence of a suitable host from chemical, visual, or other physical stimuli they leave their vantage point or shelter and move toward the source of the stimulus. Many species of ticks employ some of both types of behavior. The host-seeking behavior of the blacklegged tick, *Ixodes scapularis* Say, tends to be more of the sedentary ambushing sort, whereas lone star ticks, *Amblyomma americanum* (L.), are strongly attracted to carbon dioxide that emanates from hosts during respiration (Wilson et al. 1972) and may be best described as hunters.

Adult ticks of various species, such as *I. scapularis*, *I. neitzi* Clifford, Walker and Keirans, *I. persulcatus* Schulze, *A. americanum*, and *Dermacentor variabilis* (Say) appear to have some ability to select optimum vantage points for ambushing hosts. These adult ticks may locate surfaces (e.g., grass stems) coated with substances rubbed from the pelage or external glands of hosts, or coated with residues of host urine, and then remain on or near these surfaces (Rechav et al. 1978; Carroll et al. 1995, 1996; Dobrotvorsky et al. 2000). Because many host animals repeatedly use the same trails, feeding and bedding areas, ticks that situate themselves in high host-use locations improve their odds of acquiring a suitable host. Adults of the relatively sedentary *I. scapularis* have been reported to disperse by their own locomotion as far as 10 m over a period of 3–4 wk (Carroll and Schmidtmann 1996), and may thereby encounter host-produced kairomonal residues.

In contrast to adult ticks, little is known about whether host-produced chemicals influence where nymphal ticks wait for hosts. The immature stages of *I. scapularis* feed on a wide range of vertebrate species, including birds and lizards (Spielman et al. 1985, Durden and Keirans 1996, Keirans et al. 1996). Although adult *A. americanum,* like adult *I. scapularis,* are strongly associated with white-tailed deer, *O. virginianus* (Zimmerman), their immatures will also parasitize a variety of hosts, and have been reared successfully on domestic chickens (Koch 1983). Little has been reported about nymphal tick attraction to or arrestment on substances from the coats or glands of hosts or to host urine. Arrestment occurs when a tick engaged in ambulatory activity becomes akinetic (Sonenshine et al. 1986) as a behavioral response to certain stimuli (e.g., host-produced kairomone). In laboratory bioassays, nymphs of *I. scapularis* did not show an arrestant response to urine excreted by white-footed mice, *Peromyscus leucopus* (Rafinesque), a principal host of immature blacklegged ticks (Carroll 1999a). However, nymphs of a similar species, the taiga tick, *I. persulcatus,* were attracted to kairomonal constituents in canine hair (Naumov and Vitlin 1995). Nymphs of *A. americanum* are readily attracted to sources of carbon dioxide (Wilson et al. 1972), but their responses to other host-produced chemicals are poorly understood. The purpose of this research was to evaluate some host-produced substances for inducing arrestant activity in nymphs of *I. scapularis* and *A. americanum,* and thereby gain insight as to whether the nymphs of these two medically important species might choose host ambush sites by means of chemical cues.

MATERIALS AND METHODS

Ticks.—Nymphs of *I. scapularis* and *A. americanum* were collected by flagging during May and June in Prince George's County and Queen Anne's County, Maryland. Ticks were maintained at 22°C, 97–99% RH and a photoperiod of 16:8 (L:D) h. Adult *I. scapularis* were collected during the fall in Prince George's County and maintained at 7°C, 97–99% RH and a photoperiod of 11:13 (L:D) h.

Individual ticks used in bioassays were chosen based on their physical integrity (no missing appendages) and motility when removed from storage vials.

Substances.—To obtain samples of substances associated with avian hosts, feathers were removed from 2 male 3-wk old white leghorn chickens. Feathers were removed from the back and wings of the chickens, placed in sealed plastic bags and stored at −15°C. Canine coat substances were obtained from hair clipped from the flanks of 14 mature dogs (4 male, 10 female) kept under uniform conditions and fed identical diets by Auburn University School of Veterinary Medicine, Auburn, Alabama. The hair samples were placed directly in sealed plastic bags, which were kept at −15°C. The interdigital glands of white-tailed deer are located between the toes of the deer, and their secretions are deposited on the substrate and leaf litter. Interdigital gland samples were obtained from hunter-killed deer at a hunter check-in station in Anne Arundel County, Maryland. The hind legs of deer were removed just above the tarsal joint, sealed in plastic bags and frozen at −15°C.

Bioassays.—A 1 μl micropipette was inserted vertically in each end of a rectan-

Table 1. Numbers of *I. scapularis* and *A. americanum* nymphs on micropipettes rubbed with chicken feather substances 24 h after nymphs were released on clay islands with treated and untreated micropipettes[a].

	Treatment	Control	χ^2	*P*
I. scapularis	19	6	6.76	<0.05
A. americanum	13	11	0.16	>0.05

[a] Thirty nymphs of each species of tick were tested against mixed feather samples from chickens.

gular clay block (2.5 cm long, 1 cm wide, 1 cm high) centered in a plastic petri dish (3.5 cm diameter, 1 cm high) containing water. The petri dish with the micropipettes was placed in a larger petri dish (9 cm diameter, 1 cm high) containing water, which was in turn placed in a transparent Plexiglas glove box (65 by 85 by 45 cm) containing water 0.5 cm deep. The water confined ticks to the clay islands and provided a high relative humidity (≈95%) in the glove box. Capillary tubes (1 mm diameter, 10 cm high) were substituted for the micropipettes when adult ticks were tested.

Feathers or canine hair samples were rubbed between the thumb and forefingers of a vinyl-gloved hand, after which the apical half of one micropipette was rubbed between the gloved fingers. The micropipette at the opposite end of the clay island was rubbed similarly between the thumb and the forefinger of a clean glove. When adult *I. scapularis* were tested, only the apical 1 cm of the capillary tube was rubbed.

About 5 min after interdigital gland samples were removed from the freezer, they were warmed with a hair dryer for ≈1 min. Glandular substances were transferred by rubbing the thumb and forefinger of a vinyl-gloved hand between the toes of the leg sample and then on the basal half of a micropipette. The basal rather than the apical portion of the micropipettes was treated in the interdigital gland bioassays, because in nature interdigital gland substances are deposited on the substrate.

A nymph was released singly on the midpoint of a clay island. The location of the nymph was recorded at 1, 18 and 24 h after release. Ticks that were found to have fallen or crawled into the water during the 2 h after release or overnight were replaced on midpoints of the clay islands. Clay island and petri dish units were washed in soapy water and rinsed with clean water after every test. Thirty *I. scapularis* and 30 *A. americanum* nymphs were tested against feather substances. Ten *I. scapularis* nymphs were tested against hair substances from each of 14 dogs. An additional 10 to 20 *I. scapularis* nymphs were tested against hair substances from 2 dogs that produced extreme results in the initial tests. To confirm kairomonal activity in the canine samples (Carroll 1999b, Dobrotvorsky et al. 2000) and to compare the behaviors with nymphal responses, 10 female and 10 male *I. scapularis* were tested against substances from 10 of the same hair samples tested against nymphs. Some samples were tested against adults first and others against nymphs first. Thirty *I. scapularis* nymphs were tested against interdigital gland substances from each of 2 white-tailed deer does.

Data were analyzed by chi-square 2 × 2 contingency tables where responses of each tick were considered independent.

RESULTS

After their release on the clay islands, nymphs of both species tested against substances from feathers, interdigital glands and canine hair wandered up and down the micropipettes. At 1 h after their release, nymphs were often still active and showed no tendency to be on either the treated on untreated micropipettes. By the next morning (18 h after release), nymphs were largely akinetic. Numbers of *I. scapularis* that

Tal [illegible] ers of *I. scapularis* on micropipettes (or capillary tubes for adults) rubbed with dog hair subst [illegible] ıfter the ticks were released on clay islands with the treated and untreated micropipettes.

	n	Treatment	Control	χ^2	*P*
nymphs	140	44	78	9.5	<0.05[a]
male	100	70[b]	15	35.6	<0.05
female	100	86	7	67.2	<0.05

[a] Differed from expected equal distribution between treatment and control, indicating possible tendency to avoid treatment (canine hair substances).

[b] Some ticks remained on clay block or fell or crawled into water moat, so treatment plus control numbers may not equal n.

became akinetic on the apical portions of micropipettes treated with substances from feathers were significantly greater ($X^2 = 5.4$, $P < 0.05$) than those on the untreated micropipettes (Table 1). No such arrestant response was observed with nymphs of *A. americanum*, with 13 nymphs on treated micropipettes and 11 on untreated ones. Locations of nymphs at 24 h after release differed little from those at 18 h after release.

Canine hair substances were not observed to elicit arrestment among nymphs of *I. scapularis* when data for the samples from all 14 dogs were pooled (Tables 2–3). Instead there was a significant avoidance ($X^2 = 8.2$, $P < 0.05$) of the treated micropipettes. Samples from 2 dogs produced markedly opposite results. When *I. scapularis* nymphs were tested against hair substances from the hair of dog 9656, 19 of 30 nymphs were on treated micropipettes, whereas 4 of the ticks were on the untreated (control) micropipettes. In contrast, none of the 20 *I. scapularis* nymphs tested against hair substances from dog 9334 were on the treated micropipettes 24 h after their release on the clay island. High levels (75–90%) of both male and female *I. scapularis* showed an arrestant response to substances from the same canine hair samples tested against the conspecific nymphs (Table 3). Adults responded to substances from the hair of dogs of both sexes.

Nymphs of *I. scapularis* did not exhibit an arrestment response to interdigital gland substances from white-tailed deer does. Thirty nymphs were on treated micropipettes and 23 on untreated micropipettes ($X^2 = 0.77$, $P > 0.05$).

DISCUSSION

The responses of the *I. scapularis* nymphs to the chicken feathers indicate that at least certain host species can elicit arrestment among individuals of this life stage. A variety of bird species are reported to serve as hosts for *I. scapularis* nymphs (Anderson and Magnarelli, 1984, Anderson et al. 1985, Battaly et al. 1987, Durden and Keirans 1996, Keirans et al. 1996). Host-seeking nymphs of *I. scapularis* occur primarily in the leaf litter and forest floor where some species of resident birds regularly forage. Repeated foraging or territorial activity by birds at a location would cause oils and other substances on feathers to rub off on fallen leaves and forest floor debris. Thus, it may reward a host-seeking nymph to remain near feather-associated chemical residues on leaf litter. It may be that arrest-

Table 3. Percentage of *I. scapularis* showing an arrestant response to canine hair samples.

Sex of Dog	Nymphs	Females	Males
female	31% (n = 10)[a]	90% (n = 7)	80% (n = 8)
male	33% (n = 4)	77% (n = 3)	75% (n = 2)

[a] n = number of hair samples from different dogs that were tested against 10 ticks each.

ment in laboratory bioassays highlights a basic response of ticks to host odors that signal ticks to go no further, as if they were actually on a host. If that were the basic unit of behavior, it would account for improved host ambush site selection. Lone star tick immatures will use avian hosts in nature and have been reared on domesticated chickens in the laboratory (Koch 1983). These findings reveal basic differences in how host-seeking nymphal and adult *I. scapularis* and *A. americanum* respond to host-produced substances. Unlike *I. scapularis,* lone star ticks are equipped with eyes (all host-seeking stages) and a rapid gait suited to a more hunting type of host finding (Waladde and Rice 1982). It is, therefore, not surprising to observe different responses by both species to the same chemical stimuli. The results of the bioassays with feathers show that arrestment induced by host-produced kairomones does occur in *I. scapularis* nymphs. However, the lack of the response by the nymphs to interdigital gland substances differs from adult conspecifics, which were strongly arrested by interdigital gland substances from both sexes of deer (Carroll 2001). Interdigital gland substances are deposited directly by deer on the stratum where host-seeking *I. scapularis* nymphs occur. Most adult *I. scapularis* feed on white-tailed deer, but larvae and nymphs will also feed on deer if given the opportunity. Further investigations, focused on rodent and lizard hosts, are needed to ascertain whether chemically mediated behavior plays an important role in host-finding by *I. scapularis* and *A. americanum* nymphs.

Responses of *I. scapularis* nymphs to canine hair samples showed considerable variation. Against most canine hair samples *I. scapularis* nymphs responded indifferently or avoided them, with little indication of arrestment. However, there was a significant arrestant response to one canine sample and apparently complete avoidance of another sample. In contrast, adult *I. scapularis* of both sexes showed high levels of arrestment to the same canine hair samples in bioassays. Any of several explanations may account for this discrepancy. Nymphs of *I. scapularis* may have less need to relocate themselves to areas frequented by particular species of vertebrates than adult ticks and may lack a sophisticated mechanism to exploit host-produced chemical cues. A broad array of hosts from small to large mammals (Main et al. 1982, Durden and Keirans 1996, Keirans et al. 1996), birds and even lizards suffice as hosts for *I. scapularis* nymphs. Nymphs of *I. scapularis* may be most responsive to host species not tested. An unfed nymph starts seeking a host near where it dropped from its larval host, probably within the home range of that host and in an area frequented by that host species. An adult *I. scapularis* starts seeking a host near where it dropped from its nymphal host, which may be a species unsuitable for adult feeding (adults feed on medium to large mammals). Thus, adult ticks appear to benefit more from relocating themselves to where large hosts are. This might be reflected in the difference in mobility between these life stages. Adult *I. scapularis* can actively disperse ≥10 m in a few weeks, whereas nymphs of the same species have been reported to move 5 m (Carroll and Schmidtmann 1996). In order to exploit chemical cues left on vegetation and the substrate by hosts (Carroll et al. 1996), a tick must have the locomotory capability to find them, and the effort in terms of energy and risk must be commensurate with the tick's chances of acquiring a host. Depending on the degree to which a tick searches for host-produced residues in its microenvironment, such host finding behavior could also be considered a form of hunting, albeit different from a tick rushing upwind in a carbon dioxide gradient emanating from a resting host (Waladde and Rice 1982). Furthermore, we cannot assume that a tick wanders continuously until it finds a residue. Ticks may well wait at random vantage points for a time, and, if no hosts pass by, resume wandering. Hence, host-seeking ticks are not found just along trails and deer beds.

Perhaps in differently designed bioassays more arrestment may have been observed. In any case more bioassays of substances associated with rodent (e.g., white-footed mice) and lizard (e.g., shinks) hosts are warranted, and the threshold activity levels of host-produced kairomones need to be quantified.

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TWO NEW SPECIES OF OPIINAE (HYMENOPTERA: BRACONIDAE) ATTACKING FRUIT-INFESTING TEPHRITIDAE (DIPTERA) IN WESTERN KENYA

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Abstract.—Two new species of Opiinae are described, ***Rhynchosteres mandibularis*** and ***Fopius okekai***. Both were reared from puparia of fruit-infesting ceratitidine Tephritidae collected in western Kenya. The placement of these two species relative to the genera *Fopius* Wharton and *Rhynchosteres* Fischer is discussed, with emphasis on the transitional form of the clypeus. Arguments are presented for inclusion of these species in *Rhynchosteres* and the *Fopius desideratus* (Bridwell) species-group, respectively. This represents the first host record for the genus *Rhynchosteres.* Evidence is presented that suggests similarity in function has lead to convergence in shape of the ovipositor tip in certain Opiinae and Doryctinae.

Key Words: parasitoids, fruit, *Fopius, Rhynchosteres, Ceratitis,* Araceae, Flacourtiaceae

Fruit-infesting Tephritidae support a diverse array of parasitoids (Clausen et al. 1965, Hoffmeister 1992, Hoffmeister and Vidal 1994, Sivinski et al. 1998, Wharton et al. 2000). Among the best-studied of these are members of the opiine Braconidae. Opiines oviposit in the host egg or larval stage and emerge from the puparium. About 100 species of opiines have been recorded as parasitoids of fruit-infesting Tephritidae, largely in association with biological control programs (Silvestri 1914; Clausen 1978; Fischer 1971; Wharton 1997, 1999; Ovruski et al. 2000).

The opiine parasitoids of tephritids are particularly diverse in the Afrotropical Region, with several genera and species-groups represented (Fischer 1987, Wharton 1997). The apparent high diversity may in part reflect a sampling bias since extensive rearings of both wild and commercial fruits, focused specifically on parasitoids, have been conducted on several occasions (Silvestri 1914, Bianchi and Krauss 1937, van Zwaluwenburg 1937, Clausen et al. 1965, Steck et al. 1986). Nevertheless, recent rearings of wild fruits in Kenya, as well as the examination of incompletely identified material from older collections, suggest that our knowledge of the diversity of parasitoids in this host system is far from complete.

To increase our understanding of both the alpha and beta diversity of Afrotropical tephritid parasitoids, we describe two species whose clypeal morphology is somewhat intermediate between members of the genus *Fopius* Wharton and those of the genus *Rhynchosteres* Fischer. We also discuss the potential impact of the discovery of these species on existing classifications proposed or used by Fischer (1987, 1999), van Achterberg and Maetô (1990), Wharton (1997), and van Achterberg (1999).

MATERIALS AND METHODS

Primary types and other material used for comparison in the present study came from the following institutions and individuals: The Hungarian Natural History Museum, Budapest, Hungary (J. Papp); Texas A&M University Insect Collection, College Station, Texas, USA (TAMU); Bernice P. Bishop Museum, Honolulu, Hawaii, USA (G. Nishida, K. Arakawa); International Centre of Insect Physiology and Ecology, Nairobi, Kenya (ICIPE); Koninklijk Museum voor Midden Afrika, Tervuren, Belgium (E. De Coninck); and National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (D. Smith). Additionally, samples of wild fruits were collected throughout Kenya from 1998–2000, and processed in the laboratory to obtain emerging flies and parasitoids. Kenyan specimens used in this study were obtained primarily from Kakamega (western Kenya), the Kenyan Highlands around Nairobi, and the coastal region north and south of Mombasa. Collected fruits were held in cages above sand until tephritid flies emerged to pupate in the soil. Puparia were hand-sorted from the soil after about 2 weeks, and held in separate cages for emergence of adult flies and wasps. Field-collected fruit samples yielding the parasitoids described here were processed at ICIPE in Nairobi. Both of the species described below were reared from tephritid puparia collected in Kakamega. This study represents a collaborative effort, with the senior author assuming primary responsibility for preparation of the species descriptions and the junior author primarily responsible for the discussion of ovipositor and clypeal morphology.

Terminology for the descriptions follows Sharkey and Wharton (1997) and Wharton (1997). Additionally, details of the ovipositor tip are important in distinguishing species and possibly species-groups within the Opiinae. The species described here have what has been referred to as a double dorsal node (Wharton 1997). However, this is a general description that does not adequately describe the differences in detail among species and species-groups. In the type species of *Diachasmimorpha* Viereck, for example, the double dorsal node is delimited basally by an abruptly elevated section that tapers gradually to the apex (Wharton 1997, figs. 87, 88). Near the middle of this tapered section, there is a second elevation that is weakly excavated on its basal face. In the species described here, the double dorsal node has a different appearance since it lacks the basal excavation on the second node (Fig. 15). To differentiate the two conditions, we describe the form in the species treated here as a dorsal node with a more distally placed secondary tooth. Quicke et al. (1992) also described a double dorsal node in doryctine Braconidae, suggesting that the distinctively shaped apex of the dorsal valve of the ovipositor provided a synapomorph for the Doryctinae. The shape of the nodes in the two species described below differs from those of the typical doryctines figured by Quicke et al. (1992).

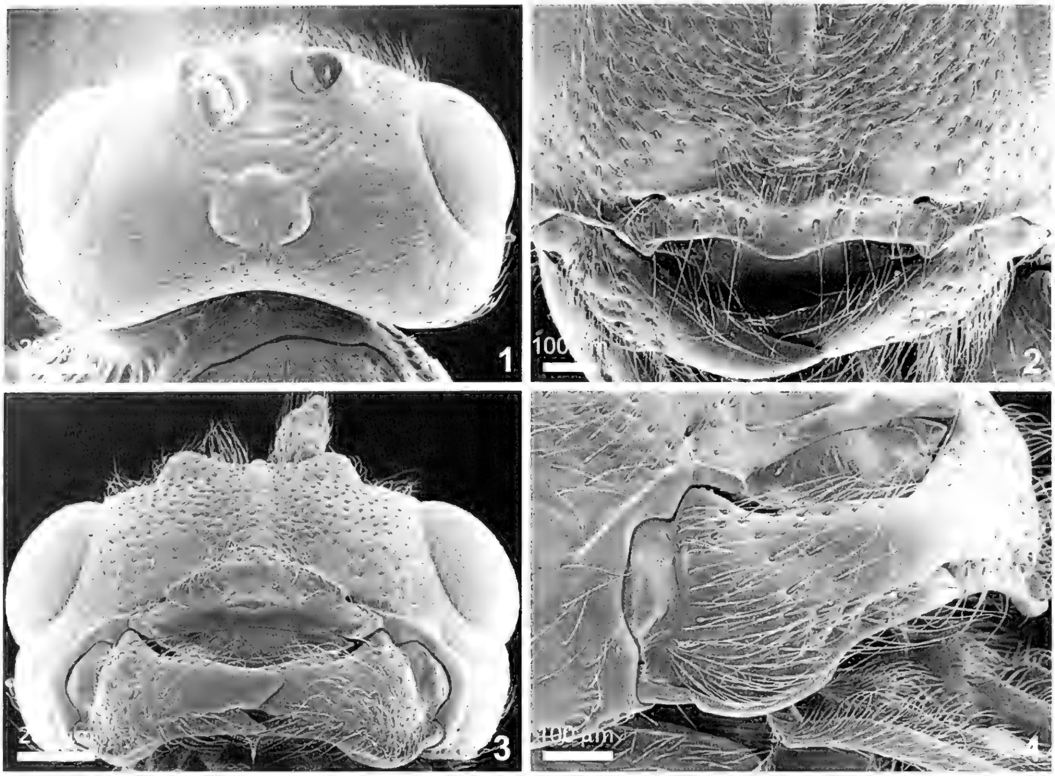
RESULTS AND DISCUSSION

Morphology of the ovipositor.—The distinctive doryctine double dorsal node was not found in any of the other cyclostomes nor in any of the non-cyclostome braconids examined by Quicke et al. (1992). The doryctine double dorsal nodes tend to be excavated on the apical face, whereas the opiine nodes are usually excavated or truncated on their basal face. However, as demonstrated here for opiines as well as in a few of the typical doryctines figured by Quicke et al. (1992), the forms converge in their reduced states (e.g., when the excavated surfaces and marginal ridges are less distinct). The condition described here for *Fopius* is thus somewhat intermediate between that found in some of the doryctines figured by Quicke et al. (1992) and those opiines previously described as having a double dorsal node by Wharton (1997). While the findings of Quicke et al. (1992) represent an important advancement in our understanding of doryctines, more detailed surveys are obviously needed to determine the extent to which the shape and number of nodes can be used unambiguously as diagnostic features for higher taxa. The nodes found on dorsal valves of various braconids and ichneumonids most likely represent reductions from the elaborately sculptured valves of siricoids, but it appears as if different structural elements may have been lost in the doryctines relative to the opiines. The end result is convergence in form, possibly for the same general function.

The mechanics of drilling into hard substrates have been recently described in superb detail by Vincent and King (1996), and a good overview of the morphology of the ovipositor in Hymenoptera is provided by Quicke et al. (1994). As pointed out by both Vincent and King (1996) and Quicke et al. (1999), dorsal nodes and ventral serrations are important attributes for species drilling through wood. Quicke et al. (1999), summarizing previous findings on the structure and function of the ovipositor, observed that endoparasitic ichneumonoids almost always have the dorsal node reduced and typically have less well-developed ventral serrations. However, the dorsal node is clearly well-developed in the species described below, as it is in several other opiines attacking fruit-infesting Tephritidae. The ventral serrations in opiines do tend to be less extensive than in most doryctines, but are still well developed in species of *Fopius* and *Diachasmimorpha* attacking late instar larvae embedded in fruit. Since some endoparasitoids (such as these opiines) must also drill to locate hosts, it is thus not surprising to find similar structures in these species. If dorsal nodes and ventral serrations are associated more with drilling through substrates than with developmental phenomenona such as endoparasitism and ectoparasitism, we should expect to find them in other endoparasitoids that must drill through solid (or at least firm) substrates to find hosts.

Morphology of the clypeus and the transition from *Fopius* to *Rhynchosteres*.—Variation in the clypeal morphology of opiine Braconidae has received considerable attention in the development of classifications for these wasps. Fischer (1972), for example, used the relative size of the clypeus and the presence of apical tubercles as the principle diagnostic features for genera within his subtribe Biosterina. He also used some of the same character states for differentiating subgenera of *Opius* as well as other genera outside the tribe Opiini. Wharton (1988, 1997) provided additional details regarding the morphology of the opiine clypeus and its utility in constructing classifications.

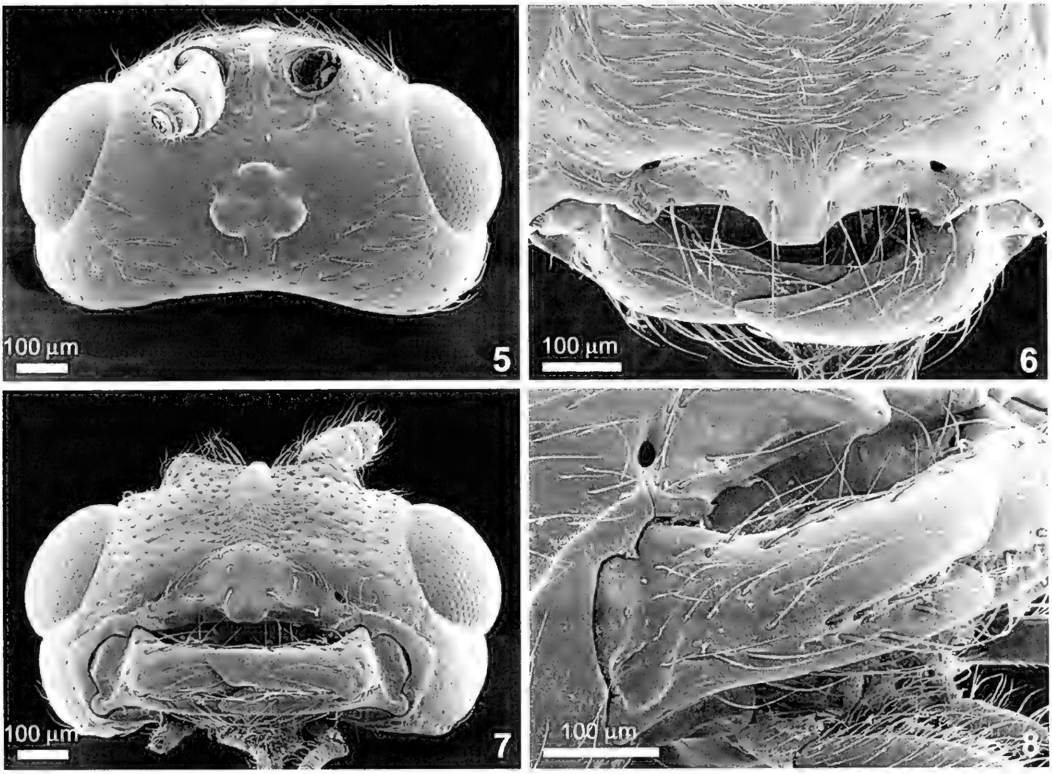
Rhynchosteres was described by Fischer (1965) for three Afrotropical species with elaborate modifications of the clypeus and varying degress of exposure of the underlying labrum. Wharton (1987) initially described *Fopius* as a subgenus of *Rhynchosteres* Fischer, noting a number of similarities between the two despite obvious differences in the form of the clypeus. Wharton (1987) also noted that within *Fopius* s. s., the clypeus was somewhat plastic, showing variation among species in protrusion of the ventral margin. Van Achterberg and Maetô (1990) elevated *Fopius* to generic status, stating that the strongly protruding clypeus of *Rhynchosteres* was sufficient to maintain the two taxa as distinct, and suggesting that any similarities were symplesiomorphs. Van Achterberg and Maetô (1990) concluded that *Fopius* was more closely related to *Pseudorhinoplus* Fischer and *Diachasmimorpha* than to *Rhynchosteres*. Wharton (1997, 1999) maintained *Fopius* as a separate genus, segregated and briefly diagnosed several species-groups, but noted that members of the *Fopius desideratus* (Bridwell) species-group shared a number of putative apomorphic features with members of the genus *Rhynchosteres*. Quicke et al. (1997) and Fischer (1999) have further discussed the relationships and classification of this group of tephritid parasitoids but only in general



Figs. 1–4. *Rhynchosteres mandibularis*, head. 1, Dorsal view. 2, Frontal view centered on face. 3, Frontal view centered on mandible and labrum. 4, Oblique view showing rounded basal lobe of mandible and medially thickened, weakly up-turned clypeus.

terms since they treated only a few of the included species.

In the type species of *Rhynchosteres*, the middle portion of the clypeus is nearly tubular and protrudes like an inverted gutter from the middle of the face. As noted by Fischer (1965), van Achterberg (1983), and Wharton (1997), however, the shape of the clypeus varies among the described species. This variation in the structural details of the clypeus makes it challenging to define unambiguously the specific character state that supports the monophyly of *Rhynchosteres*. All five previously described species have the clypeus bulging medially. In *R. microps* Fischer, *R. tuberculatus* van Achterberg, and *R. tubiformis* Fischer, the protruding part of the clypeus is thin-walled, with a tunnel-like cavity varying from ventrally-directed to anteriorly-directly in an apparent transition series. In *R. clypeatus* (Bridwell) and *R. brunigaster* Fischer, however, the clypeus is thickened ventral-medially, revealing a weakly excavated, polished surface. The two species described below exhibit clypeal modifications that tend to blur the distinctions between *Rhynchosteres* and other opiine genera, but in different ways. In the newly discovered species reared from *Rawsonia* fruits, the clypeus is short and the ventral margin is thickened, slightly upturned, and weakly protruding medially (Figs. 2–4, 9). The clypeus in this species clearly resembles that of *R. clypeatus*, but is less obviously protruding and consequently less obviously a member of *Rhynchosteres*. In the second species described below, reared from *Culcasia* fruits, the clypeus retains its full height along the midline as in *Fopius* s. s., but the ventral mar-



Figs. 5–8. *Fopius okekai,* head. 5, Dorsal view. 6, Frontal view centered on clypeus. 7, Frontal view centered on mandible. 8, Oblique view showing partially exposed labrum and unmodified mandible.

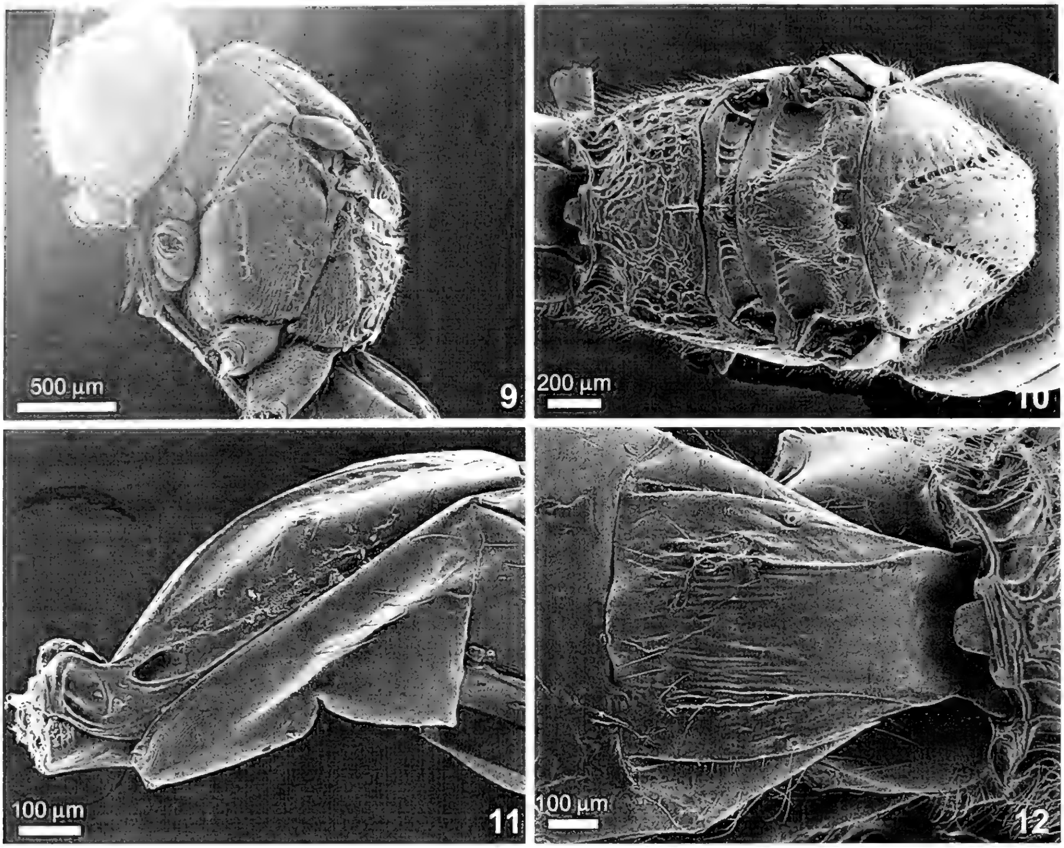
gin is excavated on either side of the midline, thus exposing a portion of the labrum (Figs. 6–8). Lateral shortening may not be a prerequisite for the development of the tube-like medial modifications seen in the *microps-tuberculatus-tubiformis* series, but would certainly facilitate it.

The discovery of the two species described here will almost certainly require a reassessment of the generic status of *Fopius,* and minimally a transfer of the *desideratus* species-group to *Rhynchosteres.* The primary purpose of the present paper, however, is to make the names available so that further work on their biology and relationships can proceed. Thus, one of the two species described below is tentatively placed in the *Fopius desideratus* species-group and the other in *Rhynchosteres.* Shared features possessed by known species of *Rhynchosteres* and the *desideratus* group include transversely striate frons (usually forming a crescent-shaped pattern), a double dorsal node on the ovipositor, and a decrease in density of setae on the ovipositor sheath (Figs. 1, 5, 14, 15). Unlike members of the genus *Diachasmimorpha* (as defined by Wharton 1997), the species of *Fopius* and *Rhynchosteres* possess an oblique groove/ridge on the propleuron. They also have a distinct post-pectal carina and a small second submarginal cell from which the m-cu cross-vein is excluded. The latter features are homoplastic within the Opiinae, but are useful for recognition of these genera.

Rhynchosteres mandibularis Kimani-Njogu and Wharton, new species

(Figs. 1–4, 9–12, 14, 15, 17, 18)

Types.—Holotype ♀: Top label = "KENYA: Western Prov. Kakamega,



Figs. 9–12. *Rhynchosteres mandibularis.* 9, Lateral view of head and mesosoma. 10, Dorsal view of mesosoma. 11, Lateral view of petiole showing deep laterope. 12, Dorsal view of petiole.

0°13.1′N, 34°54.06′E 3.viii.1999 R. Copeland". Second label = "reared from Tephritidae in fruits of Rawsonia lucida". Third label = "collection # 217 ICIPE/USAID rearing program". Deposited in National Museums of Kenya, Nairobi. Paratypes: 4 ♀, 2 ♂, same data as holotype, deposited at ICIPE and Texas A&M University.

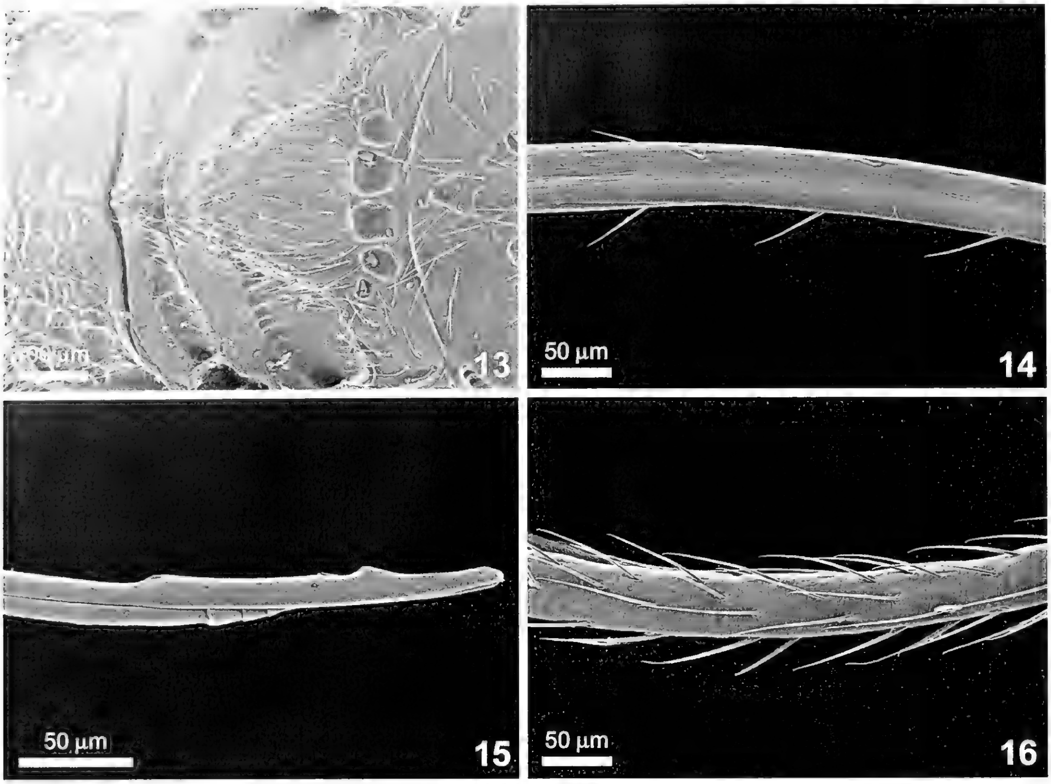
Diagnosis.—This species closely resembles *R. clypeatus* in many respects, but the mesosoma is distinctly darker in *mandibularis.* In *clypeatus,* the median tooth (or tubercle) of the clypeus is dorsally displaced relative to the remaining portion of the ventral margin. In *mandibularis,* however, the ventral-median section of the clypeus (in frontal view, Fig. 2) extends slightly ventrad the lateral margin. This new species can be separated from nearly all other opiines placed in either *Fopius* or *Rhynchosteres* by the possession of a rounded, thickly carinate lobe at the base of the ventral margin of the mandible (Figs. 3, 4). The rounded form of this structure is completely different from the more truncate or tooth-like lobe found in *Biosteres* s.s. A basal lobe is also found in *clypeatus,* but is not quite as rounded, nor as thickly carinate. The striate frons and double dorsal node on the ovipositor are identical to features found in members of the *Fopius desideratus* species-group. Unlike *mandibularis,* however, previously described members of the *desideratus* group do not have the clypeus shortened and the labrum broadly exposed. The clypeus of *mandibularis* is neither as protruding nor tunnel-shaped as in described species of *Rhynchosteres*, though it approaches the form of the clypeus in *clypeatus*, and is similarly shortened.

Description.—Female. *Length:* 4.0–5.0 mm.

Head: 1.45–1.50 times broader than long; 1.35–1.40 times broader than mesoscutum. Face (Figs. 2, 3) densely setose and punctate, punctures mostly discrete with little or no indication of rugosity, setae long, mostly decumbent and medially directed, those near inner margin of eye more ventrally directed and less decumbent; midridge polished, prominent, distinctly elevated, gradually narrowing dorsally and extending between toruli. Distance between toruli shorter than distance from torulus to eye. Frons (Fig. 1) punctate laterally and between toruli, punctures confluent or nearly so on inner side of toruli; frons medially (including at least part of ocellar field) with crescent-shaped striae. Impressed line bordering ocellar triangle largely obscured by transverse striae. Vertex (Fig. 1) smooth, highly polished on either side of ocelli; sparsely punctate laterally near compound eyes and posteriorly along occiput. Occipital carina in lateral view (Fig. 9) prominent, extending dorsally from base of mandible to a point just above middle of eye. Clypeus in profile (Fig. 9) weakly bulging dorsomedially; in frontal view (Figs. 2–4) with ventral margin protruding medially; ventral margin of clypeus thickened; labrum broadly exposed between somewhat shortened clypeus and ventrally deflected mandibles; setae on clypeus erect or nearly so, weakly directed ventrally. Eye 3.5 times longer than temple, with a few, very short, scattered setae. Temples in dorsal view (Fig. 1) slightly receding, width of head at temples less than width at eyes. Antenna with 42–43 segments; roughly 4 times longer than mesosoma; first flagellomere about 0.9 times length of second. Outer surface of mandible (Figs. 3, 4) convex basally and apically, somewhat flattened medially; ventral margin with broad, rounded, densely setose basal lobe, the margin of the lobe thickly carinate. Maxillary palps much longer than height of head.

Mesosoma (Figs. 9–10): 1.35 times longer than high; 1.85–1.90 times longer than broad. Median lobe of mesoscutum setose and punctate with punctures widely scattered posteriorly, sometimes weakly rugulose near midpit. Lateral lobes impunctate medially, with scattered punctures and relatively long inwardly directed setae around margins. Notauli broad at base, narrow posteromedially, distinctly crenulate throughout length, meeting posteriorly in a clearly defined midpit that extends narrowly towards posterior margin. Midpit broadly and very shallowly depressed. Space between midpit and scutellar sulcus smooth with scattered long setae directed outwardly towards lateral lobes. Scutellar sulcus broader medially than laterally, the posterior margin with a distinct median excavation; with 5 widely spaced longitudinal ridges. Scutellum densely setose, setae directed posteriorly; distinctly but finely punctate over most of surface, punctures elongate; transverse band of rugulose sculpture present posteriorly. Metanotum with distinctly elevated median ridge. Propodeum rugose, with a short median longitudinal carina on basal 0.25 and with crescent-shaped, transverse carina usually discernible among rugose sculpture; with long, well-spaced setae laterally, nearly bare medially; propodeum separated from metapleuron by well defined crenulate groove. Metapleuron smooth, at least on dorsal half; densely covered with ventrally-directed setae. Sternaulus broad, with deep pits, crenulate throughout; extending from anterior margin of mesopleuron at least 0.75 the distance to mid coxa.

Wings (Figs. 17–18): Fore wing stigma broad, 3.8–4.0 times longer than wide; r arising slightly distad its midpoint; 2RS weakly sinuate, nearly straight, 1.4–1.5 times longer than 3RSa; 3RSa 2.5 times longer than r; 3RSb ending nearly at wing tip; (RS+M)a sinuate; (RS+M)b present, m-cu arising distinctly basad 2RS; 1M strongly bent posteriorly; 1cu-a inclivous,



Figs. 13–16. 13, *Fopius okekai,* dorsal view of mesosoma. 14, *Rhynchosteres mandibularis,* setal pattern along middle of ovipositor sheath. 15, *R. mandibularis,* apex of ovipositor. 16, *Fopius* sp. near *silvestrii,* setal pattern along middle of ovipositor sheath.

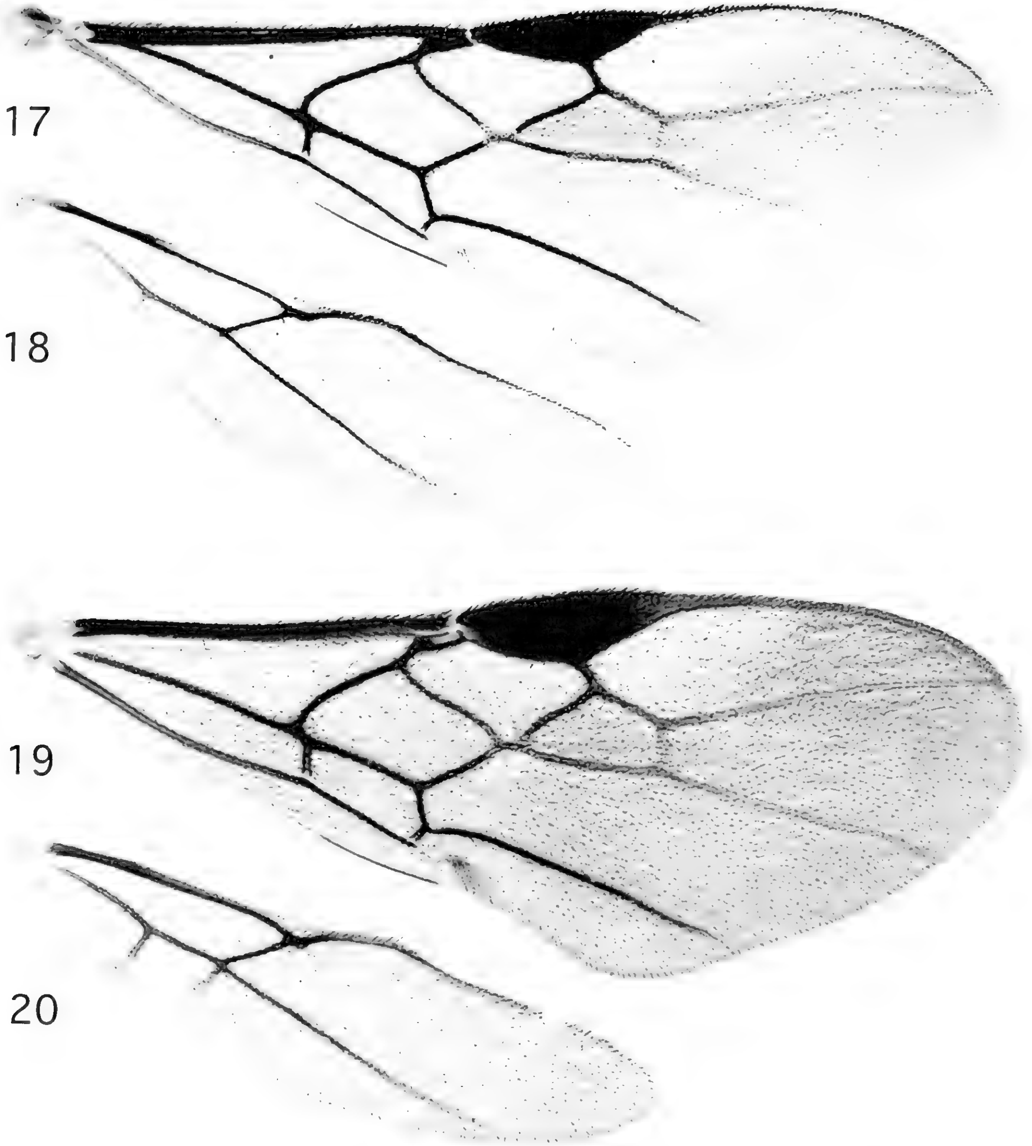
postfurcal relative to 1M. Hind wing m-cu very weakly curved towards wing base; extending nearly to wing margin as a faint crease, very weakly pigmented anteriorly, barely visible posteriorly.

Metasoma: Petiole (Figs. 11, 12) 1.5 times longer than apical width, apex 1.8 times wider than base; finely striate; dorsal carinae well-developed over basal 0.8, indistinct toward posterior margin; dorsope absent, laterope present as a deep pit. Metasoma unsculptured beyond petiole. Hypopygium strongly narrowed and pointed posteriorly but short, not greatly attenuated. Ovipositor tip (Fig. 15) with a dorsal node, and a small, more distally placed secondary tooth. Ovipositor sheath sparsely setose basally (Fig. 14), with about 3 rows of short to very short, well-spaced setae, setae more dispersed apically, with only two apparent rows; sheath longer than body, 2.5 times longer than mesosoma.

Color: Head, mesosoma, ovipositor sheath, wing veins, and last three metasomal terga brown to very dark brown; hind tibia and tarsi dorsally brown; metapleuron, propodeum laterally and most of metanotum orange; petiole, basal segments of gaster, scape, annellus, and remainder of legs yellow.

Male.—About as in female except antenna 42–45 segmented; mandibles not as strongly deflected ventrally, thus labrum only narrowly exposed; scutellar sulcus with 3 ridges; transverse carina of propodeum not discernible; metasomal terga 4 and following black.

Discussion.—The plant host is a member of the Flacourtiaceae. Three species of Tephritidae have been reared from this host



Figs. 17–20. Fore and hind wings. 17, 18, *Rhynchosteres mandibularis*. 19, 20, *Fopius okekai*.

plant in Kenya: *Ceratitis anonae* Graham, *C. rosa* Karsch var. *fasciventris* (Bezzi), and an undescribed species of *Trirhithrum* Bezzi. Only one of these (the *Trirhithrum*) was reared from the same batch of puparia that yielded the type series. These puparia were isolated from a collection of 165 fruits. The undescribed species of *Trirhithrum* (family Tephritidae) is the first confirmed host record for the genus *Rhynchosteres*.

Etymology.—The species name refers to the enlarged basal lobe of the mandible.

Fopius okekai
Kimani-Njogu and Wharton, new species
(Figs. 5–8, 13, 19, 20)

Types.—Holotype ♀: Top label = "KENYA: Western Prov. Kakamega, along Yala River Trail, 0°12.34′N, 34°53.57′E [illegible] Copeland”. Second label = “reared from Tephritidae in fruits of Culcasia falcifolia”. Third label = “collection # 639 ICIPE/USAID rearing program”. Deposited in National Museums of Kenya, Nairobi. Paratypes: 2 ♂, same data as holotype, deposited at ICIPE and Texas A&M University.

Diagnosis.—This species is recognized as a member of the *Fopius desideratus* species-group by the enlarged clypeus plus the combination of features noted in the morphology section above that are shared by *Rhynchosteres* and the *desideratus* species-group. The ventral margin of the clypeus is strongly protruding medially as a truncate tooth in this species (Figs. 6–8). A median projection is also present (though not as well developed) in *F. ottotomoanus* and *F. niger,* the two species with which it is most likely to be confused. In *okekai,* the ventral margin of the clypeus on either side of the projection is weakly concave, exposing a portion of the labrum and making the projection appear more prominent. In *okekai,* the projection is directed ventrally whereas in *ottotomoanus* and *niger* it is directed more anteriorly and thus protrudes more from the face. The mandible is normal in *okekai,* lacking the rounded basal lobe on the ventral margin found in *mandibularis.* It is also a darker species than *mandibularis,* has a more distinctly punctate scutellum, a better-developed hind wing m-cu, and a less prominent secondary tooth on the ovipositor.

Description.—Female. *Length:* 4.0 mm.

Head: 1.35 times broader than long; 1.45 times broader than mesoscutum. Face (Figs. 6, 7) densely setose and punctate throughout, pattern variable, space between most punctures greater than diameter of punctures, but some punctures nearly confluent, suggesting rugulose sculpture; setae as in *mandibularis*; midridge distinctly elevated, polished, narrower dorsally, extending between toruli. Distance between toruli almost equal to distance from torulus to eye. Frons (Fig. 5) with sculpture and setal pattern about as in *mandibularis,* but striae much weaker, not extending posteriorly to median ocellus, thus surface appearing more extensively smooth and polished. Ocellar triangle almost completely margined by an impressed line. Vertex and occipital carina as in *mandibularis.* Clypeus in profile weakly bulging dorsomedially; ventral margin of clypeus (Fig. 6) with a strongly protruding rectangular projection; labrum (Fig. 8) partially exposed between somewhat shortened clypeus and ventrally deflected mandibles; setae on clypeus sparse, at least twice as long as those in middle of face, erect or nearly so. Eye apparently bare; large, 3 times longer than temple. Temples in dorsal view receding, width of head at temples less than width at eyes. Antenna 35 segmented; roughly 3.7 times longer than mesosoma. 1st flagellomere about 0.8 times length of second. Mandible (Fig. 8) normal, outer surface distinctly convex, ventral margin without expanded lobe basally. Maxillary palps much longer than height of head.

Mesosoma (Fig. 13): 1.4 times longer than high; 1.9 times longer than broad. Median lobe of mesoscutum setose as in *mandibularis,* with unevely spaced punctures; lateral lobes with numerous, relatively long setae around margins, bare and impunctate medially. Notauli distinctly crenulate throughout, meeting posteriorly in a clearly defined midpit that extends slightly onto median lobe anteriorly as a sculptured groove, midpit with irregular sculpture. Mesoscutum otherwise as in *mandibularis.* Scutellar sulcus parallel-sided or nearly so. Scutellum uniformly setose; with deep, elongate punctures clearly visible beneath weakly decumbent setae; transverse band of sculpture distinctly rugose. Metanotum about as in *mandibularis,* with distinctly elevated median ridge but more prominently carinate lateral fields. Propodeum densely rugose, with median carina on basal 0.5 and with irregular, transverse carina discernible among rugose sculpture; setal pattern as in *mandibularis*; propodeum not distinctly separated from metapleuron laterally, the demarcation represented only by the transition across a shallow groove to the weakly sculptured dorsal portion of the metapleuron. Metapleuron and sternaulus about as in *mandibularis.*

Wings (Figs. 19, 20): Forewing stigma broad, 3.2 times longer than wide, with r arising slightly distad its midpoint; 2RS nearly as sinuate as (RS+M)a, 1.3 times longer than 3RSa; 3RSa 2.25 times longer than r; 3RSb ending almost at wing tip; (RS+M)b present and fairly long, roughly 0.2 times length of m-cu; 1M weakly curved posteriorly; 1cu-a inclivous, postfurcal relative to 1M by 0.35–0.40 its length. Hind wing m-cu reclivous, but not recurved, distinctly pigmented slightly more than halfway to wing margin.

Metasoma: Petiole 1.3 times longer than apical width; apex about 1.8 times wider than base; sculpture, dorsope, and laterope as in *mandibularis.* Metasomal terga unsculptured beyond petiole. Hypopygium as in *mandibularis.* Ovipositor tip with dorsal node and a barely perceptible, more distally placed secondary tooth. Ovipositor sheath with setae about as in *mandibularis,* with setae slightly more closely spaced in longest row; sheath distinctly shorter than body, about 1.6 times longer than mesosoma.

Color: Dark brown to black; petiole brown basally, yellow-brown apically; tegula, T2, trochantellus dorsally, and apices of fore and mid femora yellow; palps whitish.

Male.—Length 3.8–4.5 mm. About as in female except temple larger, eye 2.5 times longer than temple; antenna 37 segmented; first flagellomere 0.85–0.90 times length of second; yellow coloration on legs and metasoma slightly more extensive, with petiole completely yellow.

Discussion.—The plant host is a member of the Araceae. The type series came from a sample of tephritid puparia, isolated from 200 fruits, that also produced *Trirhithrum inscriptum* (Graham) and *T. nigrum* (Graham).

Etymology.—The species is named for Wilberforce Okeka, who assisted in the collection of fruits and identification of plants in Kakamega forest.

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This work could not have been accomplished without the logistic support and facilities provided by ICIPE and the personnel in the division of forestry in Kakamega Forest who kindly facilitated the sampling program there. We also express our thanks to Ian White and Marc DeMeyer for identification of the flies and especially to Robert Copeland for conducting and managing the sampling program. Milicent Okumu assisted with sample processing and Peterson Nderitu provided a sample of *Cucumis dipsaceus* that produced parasitoids crucial for comparison with the newly described species. Special thanks to Jim Ehrman at the Digital Microscopy Facility, Mount Allison University, Sackville, NB, Canada for doing all of the SEM work, including arranging the plates, and to Matt Buffington and Terry Junek for help with the wing figures. This work was supported primarily by USAID grant No. PCE-G-00-98-00048-00 to Texas A&M University (in collaboration with ICIPE and the African Fruit Fly Initiative) and in part by USDA/NRI (grant no. 9703184) and NSF (DEB9712543), both to Texas A&M.

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A NEW SPECIES AND NEW RECORDS OF *MICROCERELLA* MACQUART (DIPTERA: SARCOPHAGIDAE) FROM ARGENTINEAN PATAGONIA

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Abstract.—***Microcerella antonioi,* n. sp.** (Sarcophagidae), from Santa Cruz, Argentina, is described and illustrated. The following four species are recorded for the first time from Argentinean Patagonia: *Microcerella aulacophyto* Pape, *M. chilena* (Dodge), *M. penai* (Lopes), and *M. rusca* (Hall).

Resúmen.—Se describe e ilustra una nueva especie de Sarcophagidae, ***Microcerella antonioi,*** de Santa Cruz, Argentina. Asimismo se registran por primera vez para la Patagonia Argentina a *M. aulacophyto* Pape, *M. chilena* (Dodge), *M. penai* (Lopes) y *M. rusca* (Hall).

Key words: Diptera, Sarcophagidae, *Microcerella,* new species, Argentinean Patagonia

Fifteen species of *Microcerella* Macquart 1851 are presently known in Patagonia, (Pape 1996). During 1997 and 1998, several collecting trips to Patagonia were carried out by the author, and a large number of specimens of *Microcerella* were captured. A detailed study of this material revealed an undescribed species, which is herein described and illustrated. Also, several new localities in the Argentinean Patagonia are provided for *M. aulacophyto* Pape, *M. chilena* (Dodge), *M. penai* (Lopes), and *M. rusca* (Hall).

For general Sarcophagidae terminology see Lopes (1978, 1982). Illustrations were made by using a camera lucida attached to a stereoscopic microscope.

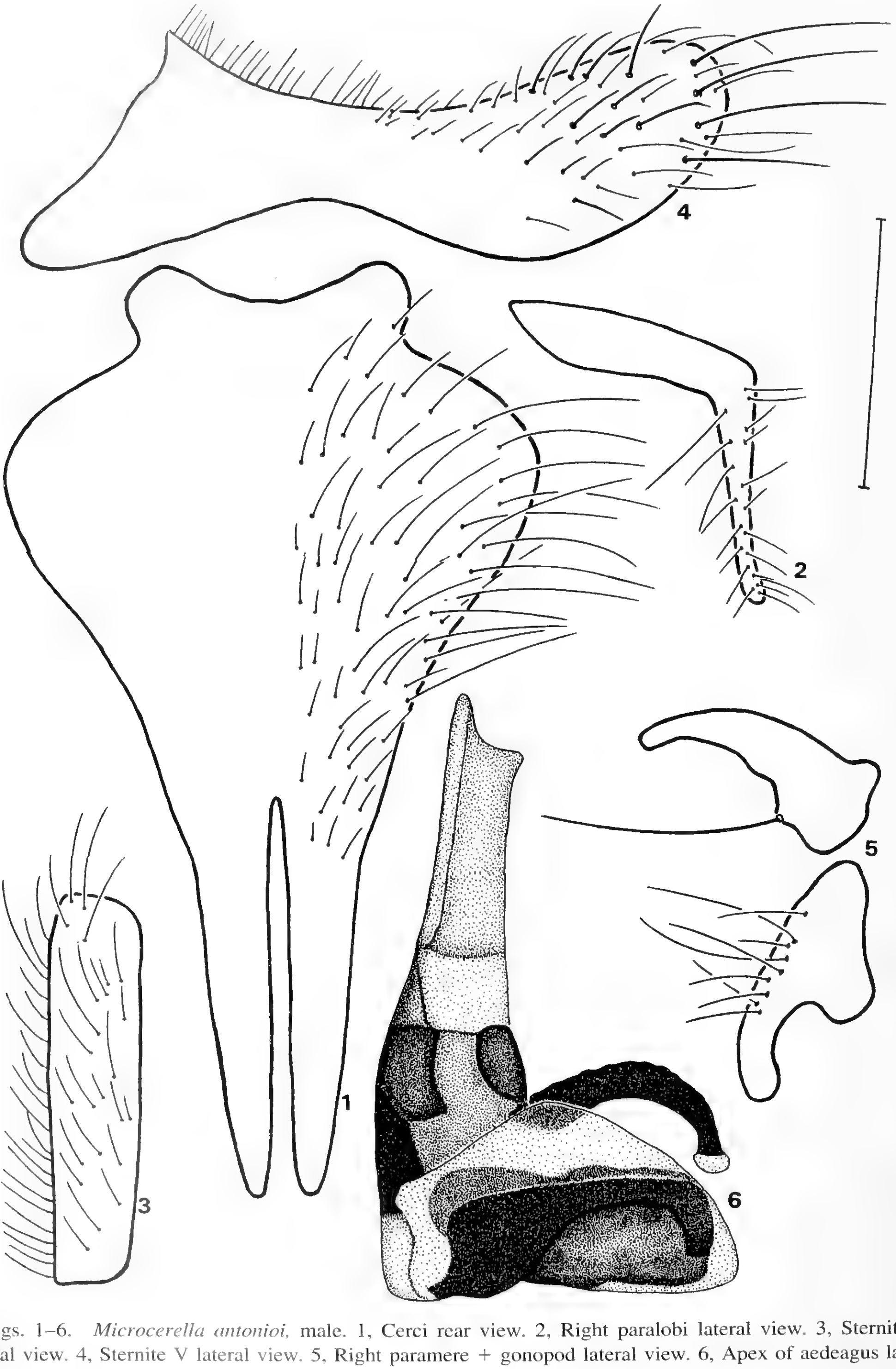
The holotype and paratypes of the new species are pinned. The holotype and some paratypes are deposited in the collection of the Museo de La Plata, Buenos Aires, Argentina. Other paratypes are deposited in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina, and Fundación Miguel Lillo, Tucumán, Argentina. The specimens of the other four species are in Museo de La Plata, Buenos Aires, Argentina.

Microcerella antonioi Mariluis, new species

(Figs. 1–6)

Diagnosis.—*Male* with a pair of preacrostichal bristles; first pair of ocellar bristles situated at center of ocellar triangle; lower part of sternopleura with spot of silvery pollinosity; scutellum without discal scutellar bristles; sternite IV without hump; sternite V without evident humps at medial part of both arms; inner border of cerci not undulated; paralobi slender; and apical and lateral plate with a single lobe.

Holotype male.—Length: 7–11 mm. *Head:* Black with silvery pollinosity, almost quadrate. Epistoma protuberant. Cheeks, clypeus, parafrontalia, parafacialia, cheek grooves, occipital fringe, and post-



Figs. 1–6. *Microcerella antonioi,* male. 1, Cerci rear view. 2, Right paralobi lateral view. 3, Sternite IV lateral view. 4, Sternite V lateral view. 5, Right paramere + gonopod lateral view. 6, Apex of aedeagus lateral view. Scale = 0.5 mm.

gena black with silvery pollinosity. Frontalia velvety black, upper part with silvery pollinosity and black hairs. Ocellar triangle black, with two pairs of the strong ocellar bristles. Parafrontalia and parafacialia with black hairs. Upper parafacialia with small hairs and low parafacialia with long hairs twice size of upper ones. Parafacialia 0.44 of distance between vibrissa. Front at narrowest part about 0.29 of head width. With 5 to 7 frontal bristles, to antennal base 4 to 5, rest pass antennal base, first pair faces backwards, all rest converge. Inner vertical bristles twice size of outer vertical bristles. Facialia black, with black hairs, lower part shining and upper part with silvery pollinosity. Antenna black, segments I and II shining black, III with brown pollinosity, arista bare. *Thorax:* Black with silvery pollinosity. In lateral view, notopleuron and mesopleuron with spot of golden pollinosity. Pteropleuron with spot of silvery pollinosity. Sternopleuron with two stigma of silvery pollinosity, one in foremost upper part around first sternopleural bristles and other at lower part. Thorax in dorsal view a bit inclined with head down and abdomen up, black with stripes of silvery pollinosity. Prescutum and postcutum with two stripes in area of dorsocentral bristles. Following marks of silvery pollinosity: all humeri; on inferior part of prescutum and one major on inferior central part of postscutum, these marks between intraalar and supraalar bristles. Postalar callus with apical spot of silvery pollinosity. Scutellum black, with three marks of silvery pollinosity, two lateral and one distal between posterior marginal lateral bristles. Acrostichals 1:0; dorsocentrals 2:3; intraalar 1:2; supraalar 1:3 Scutellum with two pairs of marginal lateral bristles, one anterior and other posterior, without discal bristles. Wings, epaulet, base of stem vein and point of union of R3 with R5 black. Subepaulet and rest of veins orange. Base of R5 with black hairs. Legs black, hind femur with row of bristles on anterior and anterodorsal sides. Middle and posterior tibiae with 2, 3 or 4 bristles on anterodorsal and posterodorsal sides. *Abdomen:* Black. In posterior view, tergite I+II without pollinosity, III to V with two marks of silvery pollinosity dorsally, with one mark of golden pollinosity laterally and other silvery pollinosity ventrally. Sternites I to V black with black hairs. Sternite IV (Fig. 3) without hump. Sternite V (Fig. 4) without evident humps at medial part of both arms. First genital segment shining black without silvery pollinosity and with six marginal bristles. Second genital segment orange reddish and with black hairs. Cercus (Fig. 1) slender, curved forward, orange reddish on proximal part, black apically, with black hairs. Paralobi (Fig. 2) slender. Apical and lateral plates of distiphallus well developed, with a single lobe (Fig. 6); styli curved, with a crest on convex border (Fig. 6).

Female.—Unknown

Distribution.—Argentina, Santa Cruz.

Type material.—Holotype ♂ and 24 ♂ paratypes from Argentina, Santa Cruz: Pto. Santa Cruz, II-1998, J. C. Mariluis; 1 paratype ♂ same locality but XI-1997, J. C. Mariluis; 2 paratype ♂ same locality but I-1998, J. C. Mariluis; 3 paratype ♂ from Argentina, Santa Cruz: Río Gallegos, I-1998, J. C. Mariluis.

Etymology.—Named after my father Mr. Antonio Leoncio Mariluis.

Discussion.—*Microcerella antonioi* is similar to *M. rusca* (Hall 1937). However, the male of *M. rusca* differs from the male of *Microcerella antonioi* by the first pair of ocellar bristles situated behind or at the same level of the two anterior ocelli, absence of preacrostichals bristles, lower part of sternopleuron with spot of golden pollinosity, scutellum with a pair of discal scutellar bristles, sternite IV (Fig. 13) with a conspicuous hump behind middle, sternite V (Fig. 14) with evident humps on both arms, cerci (Fig. 11) with inner border undulated, paralobi (Fig. 12) heavy, and apical and lateral plate of distiphallus with two lobes. No material in reference to this new species has been found in both of the most important Natural History Museums in Argentina (Museo de La Plata and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia").

Microcerella aulacophyto Pape
(Figs. 7–8)

Aulacophyto auromaculata Townsend 1919: 158 (♂, ♀; Peru: Oroya; junior secondary homonym of *Euparaphyto auromaculata* Townsend 1919); Hall 1937: 350, 360 (key; ♂, ♀; Chile: Santiago, "East side" Andes presumably near Potrerillos, Mendoza, Argentina); Lopes 1968: 57 (♂ paratype, figs. 25–27; Bolivia: La Paz, Chile: Iquique and Maniña); Lopes 1969: 7 (in catalog; Peru, Chile); Lopes 1978: 757, 758 (♂, ♀, figs. 1–9; Argentina: Jujuy, Bolivia: La Paz, Chile: Antofagasta and Iquique, Peru: Camacani and Puno); Lopes 1982: 362 (key); Lopes and Tibana 1982: 136 (Chile: Arica); Tibana and Lopes 1987: 372 (key).

Microcerella aulacophyto Pape 1990: 49 (new name for *Aulacophyto auromaculata* Townsend 1919); Pape 1996: 253 (in catalog; Argentina: no further data, Bolivia, Chile: Bíobio and Tarapacá, Peru).

Distribution.—Argentina (Jujuy and Santa Cruz), Bolivia (La Paz), Chile (Antofagasta, Arica, Bíobio, Iquique, Maniña, Santiago and Tarapacá), Peru (Camacani, Oroya and Puno).

New records.—Argentina, Santa Cruz, Pto. Santa Cruz, XII-1997, J. C. Mariluis, 9 ♂, 2 ♀; same data I-1998, J. C. Mariluis, 5 ♂, 1 ♀; same locality but II-1998, J. C. Mariluis, 45 ♂, 2 ♀; Río Gallegos, I-1998, J. C. Mariluis, 4 ♂.

Discussion.—The studied specimens agree with the description of *A. auromaculata* by Lopes (1968, 1978).

Microcerella chilena (Dodge)
(Fig. 10)

Aulacophyto chilena Dodge 1967: 679 (♂, ♀; Chile: Antofagasta, Longuén and Santiago); Lopes 1978: 757, 758 (♂ paratype, ♀, figs. 10–23, Argentina: Mendoza, Chile: Aconcagua, Alichahue, Antofagasta, Coquimbo and Curico, Peru: Camacani, Cuzco and Puno); Lopes 1982: 362 (key); Tibana and Lopes 1987: 372 (key, Chile).

Microcerella chilena: Pape 1990: 49 (combination), 1996: 254 (in catalog; Chile: Antofagasta and Santiago, Peru).

Distribution.—Argentina (Mendoza and Rio Negro), Chile (Aconcagua, Alichahue, Antofagasta, Coquimbo, Curico, Longuén and Santiago), Peru.

New records.—Argentina, Río Negro, Ruta 305, among S. A. Oeste and Pomona, 15-I-1977, J. C. Mariluis, 1 ♂; Choele-Choel, 18-I-1977, J. C. Mariluis, 1 ♀.

Discussion.—The studied specimens agree with the description of *A. chilena* by Lopes (1978).

Microcerella penai (Lopes)
(Fig. 9)

Aulacophyto penai Lopes 1978: 757, 762 (♂, ♀, figs. 28–39, Argentina: Jujuy, Bolivia: La Paz); Tibana and Lopes 1987: 372 (key; Chile: no further data); Verves 1989: 534 (list).

Microcerella penai: Pape 1990: 49 (combination), 1996: 257 (in catalog; Argentina: Jujuy).

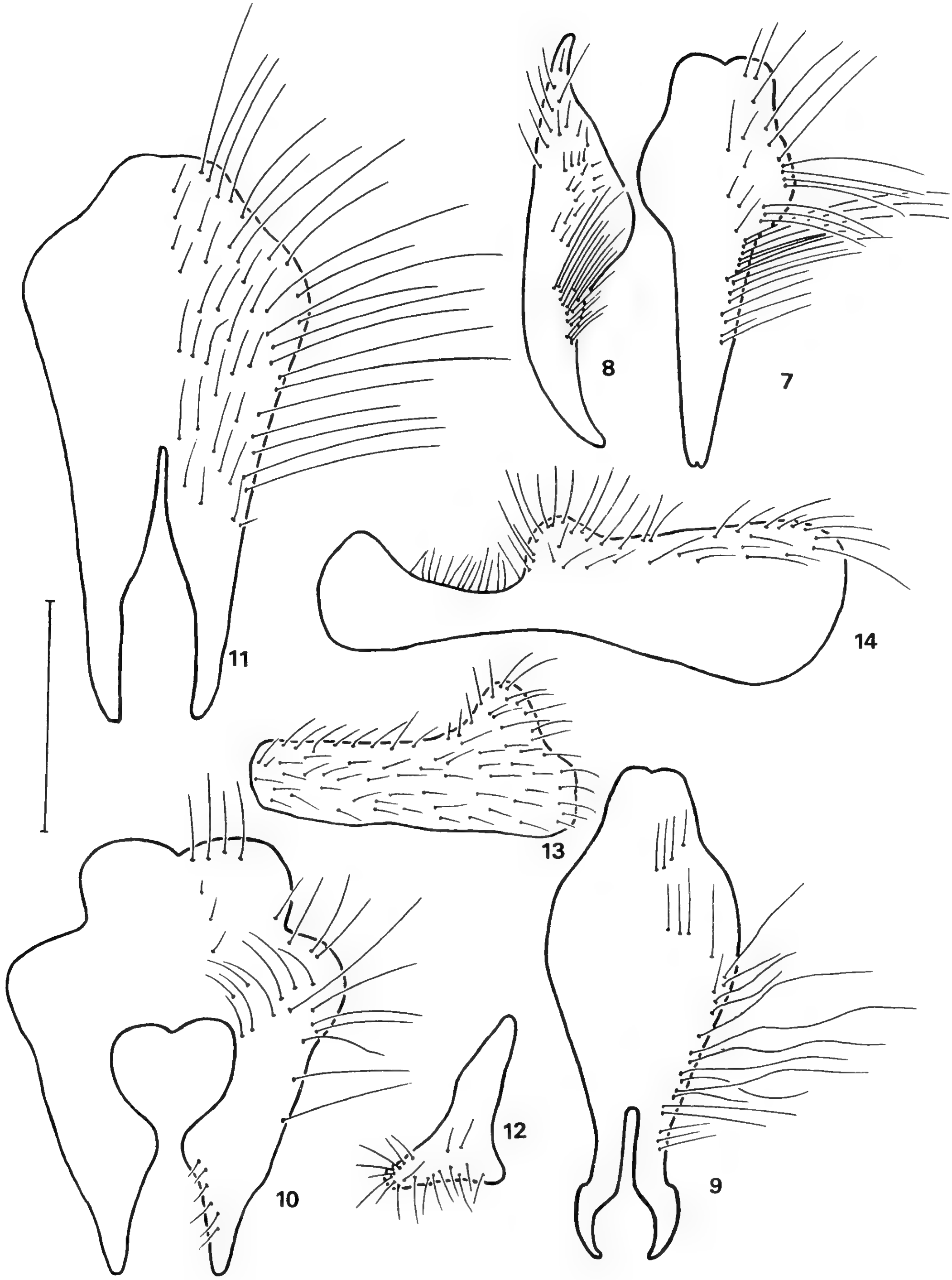
Distribution.—Argentina (Jujuy and Santa Cruz), Bolivia (La Paz), Chile.

New records.—Argentina, Santa Cruz, Pto. Santa Cruz, I-1998, J. C. Mariluis, 2 ♂.

Discussion.—The studied specimens agree with the original description.

Microcerella rusca (Hall)
(Figs. 11–14)

Aulacophyto rusca: Hall 1937: 350, 361 (♂; Argentina: Bariloche); Lopes 1969: 7 (in catalog; Argentina); Lopes 1978: 757, 758 (key); Tibana and Lopes 1987: 371, 372 (♂, ♀; figs. 6–12, Chile: Antofagasta, Cautin, Coquimbo, Curico, Malleco and Santiago).



Figs. 7–14. *Microcerella aulacophyto,* male. 7, Cerci rear view. 8, Right cerci lateral view. 9, *M. penai,* male, cerci rear view. 10, *M. chilena,* male, cerci rear view. Figs. 11–14. *M. rusca,* male. 11, Cerci rear view. 12, Right paralobi lateral view. 13, Sternite IV lateral view. 14, Sternite V lateral view. Scale = 0.5 mm.

Microc [illegible] *sca:* Pape 1990: 49 (combination [illegible] 1996: 257 (in catalog; Argentina: Río Negro, Chile: Antofagasta, Cautin, Coquimbo, La Araucanía, Maule and Santiago).

Distribution.—Argentina (Río Negro, Santa Cruz), Chile (Antofagasta, Cautin, Coquimbo, Curico, Malleco, Maule and Santiago).

New records.—Argentina, Santa Cruz, Pto. Santa Cruz, XII-1997, J. C. Mariluis, 2 ♂, 9 ♀; same locality but I-1998, J. C. Mariluis, 5 ♂, 15 ♀; same locality but II-1998, J. C. Mariluis, 57 ♂, 81 ♀; Rio Gallegos, XII-1997, J. C. Mariluis, 3 ♂; same locality but I-1998, J. C. Mariluis, 7 ♂, 8 ♀; same locality but II-1998, J. C. Mariluis, 16 ♂, 6 ♀.

Discussion.—The studied specimens concur with the description of *A. rusca* by Tibana and Lopes (1987).

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NEW SPECIES OF THE PLANT BUG GENERA *KELTONIA* KNIGHT AND *PSEUDATOMOSCELIS* REUTER (HETEROPTERA: MIRIDAE: PHYLINAE)

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Abstract.—The new phyline plant bugs, ***Keltonia wheeleri*** from Georgia and South Carolina in the southeastern United States, and ***Pseudatomoscelis nubila*** from Province Pedernales in the Dominican Republic, are described. A dorsal habitus illustration and selected scanning electron micrographs of *K. wheeleri,* male genitalia of both species, and modified identification keys, including photographs of the keyed species [*K. rubrofemorata* (Knight); *K. wheeleri,* n.sp.; *P. flora* (Van Duzee); *P. insularis* Henry; *P. nubila,* n.sp.; and *P. seriata* (Reuter)], are provided to help distinguish the new species.

Key Words: Heteroptera, Miridae, Phylinae, *Keltonia wheeleri, Pseudatomoscelis nubila,* new species, Nearctic, Neotropical

The mirid genus *Keltonia* Knight contains 12 species ranging from Massachusetts to Colorado in the United States, south to Colombia, and into the West Indies (Bahamas, Jamaica), and the genus *Pseudatomoscelis* Reuter contains three species, including the cotton fleahopper [*P. seriata* (Reuter)], ranging from southern Canada, south to Venezuela, and into the West Indies (Puerto Rico, St. Thomas) (Henry 1991). Henry (1991) revised these two phyline genera, described six new species of *Keltonia* and one new species of *Pseudatomoscelis,* and hypothesized that they represented sister genera, based on the shared stout C-shaped vesica bearing a large sickle-shaped spicule, clumps or tufts of acuminate sericeus or scalelike setae on the dorsum, one or two patches of dark bristlelike setae along the inner margin of the cuneus, and the large dark area on the membrane near the apex of the cuneus. Synapomorphies defining the species of *Keltonia* are the dorsal spots limited to the hemelytra; the conspurcate hemelytral membrane; sericeus or scalelike setae in distinct clumps and, often, in rows along the midline of the head and pronotum; the pale tibiae, with dark spots at bases of spines; and the stoutly formed, weakly twisted, C-shaped vesica, with a slender spicule and cuplike apical process. Synapomorphies defining the species of *Pseudatomoscelis* are the three or more spots on antennal segment II; the brown to black hemelytral membrane, with a black mark just posterior to the apex of the cuneus; the sericeus or scalelike setae in patches or clumps, but not in rows along midline (as in species of *Keltonia*); the stoutly formed, C-shaped vesica (lacking an apical cuplike process); and the phallotheca with a subapical spine (except in *P. nubila* n. sp.).

In this paper, I describe *K. wheeleri* to provide a name for a forthcoming paper on its seasonal history, host, and distribution (Wheeler, in preparation), and *P. nubila* to provide a name for my forthcoming list of the Miridae of the Dominican Republic. An adult dorsal habitus illustration and scanning electron micrographs of selected structures of *K. wheeleri*; figures of the male genitalia for both species; and modified keys, including photographs of species keyed in Henry (1991) [*K. rubrofemorata* (Knight); *K. wheeleri,* n. sp.; *P. flora* (Van Duzee); *P. insularis* Henry; *P. nubila,* n. sp.; and *P. seriata* (Reuter)], are provided to help distinguish the new species.

Acronyms for type depositories as follows: AMNH (American Museum of Natural History, New York, NY); CNC (Canadian National Collection, Ottawa, Ontario); TAMU (Texas A & M University, College Station, TX); and USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC).

Keltonia wheeleri Henry, new species

(Figs. 1–8, 10–13)

Diagnosis.—*Keltonia wheeleri* (Figs. 1, 8) is distinguished from all other species of the genus in having a shiny yellow dorsum (including the head, antenna, and pro- and mesofemora), a large centrally positioned fuscous spot on the hemelytra, an apically orange or red-tinged metafemur, and a fuscous or black membrane sprinkled with white spots.

Description.—*Male* (n = 10): Length 2.45–2.85 mm, width 1.02 mm. *Head* (Figs. 2, 3): Width 0.56–0.59 mm, vertex 0.34–0.38 mm. *Rostrum:* Length 0.74–0.77 mm, extending to mesocoxae. *Antenna:* Segment I, length 0.18–0.19 mm; II, 0.58–0.66 mm; III, 0.43–0.50 mm; IV, 0.37–0.40 mm. *Pronotum:* Length 0.34–0.35 mm, basal width 0.78–0.88 mm.

Female (n = 10): Length 2.50–2.72 mm, width 1.08–1.10 mm. *Head:* Width 0.56–0.59 mm, vertex 0.35–0.37 mm. *Rostrum:* Length 0.77–0.83 mm, extending to mesocoxae. *Antenna:* Segment I, length 0.16–0.19 mm; II, 0.64–0.67 mm; III, 0.43–0.51 mm; IV, 0.42 mm. *Pronotum:* Length 0.32–0.34 mm, basal width 0.82–0.83 mm.

Overall coloration shiny yellow to greenish yellow. Head, antenna, and pronotum uniformly yellowish to greenish yellow. Hemelytron yellow to greenish yellow, apical half of clavus and inner area of corium from middle of clavus to base of cuneus forming a large, dark patch or cloud. Ventral surface uniformly greenish yellow. Legs mostly yellowish green; metafemur tinged with orange or red on apical ⅓ and anterior half finely brown spotted; pale tibial spines with vague pale brown spots at bases; tarsi yellowish; claws brown. Vestiture of two types: simple, erect and semierect, pale brown setae on head, pronotum, and on greenish-yellow areas of hemelytron, simple fuscous to black setae on dark central area; and silvery sericeus or slender scalelike setae scattered on head, pronotum, and dark areas of hemelytron, a few clusters of sericeus setae along inner margins of eyes (Fig. 3), but without a median row of scalelike setae on head, pronotum, and scutellum typical of most other species in the genus.

Male genitalia: Genital capsule (Figs. 6, 7); vesica (Fig. 10); left paramere (Fig. 11); right paramere (Fig. 12); phallotheca (Fig. 13).

Etymology.—This species is named in honor of Dr. A. G. Wheeler, Jr., long-time friend, colleague, and discoverer of this attractive new species.

Host.—*Polygonella americana* (Fischer-Meyer) Small [Polygonaceae].

Distribution.—Known only from the southeastern United States (Georgia and South Carolina).

Type material.—Holotype ♂: South Carolina, Aiken Co., Henderson Heritage Pres[erve]., N. of Aiken, 30 May 1998, A. G. Wheeler, Jr., taken on *Polygonella americana* (USNM). Paratypes: GEORGIA: 2 ♀, Burke Co., Yuchi Wildlife Mgt. Area, 4 mi. NNE of Girard, 1 July 1998, AGW, on *P. americana* (USNM); 4 ♂, 2 ♀, Columbia Co., Rt. 383, E of Lewiston, 5 July 1998, AGW, on *P. americana* (USNM); 1 ♂, 5 ♀, Glascock Co., Rt. 80, NE of Gibson, 5 July 1998, AGW, on *P. americana*

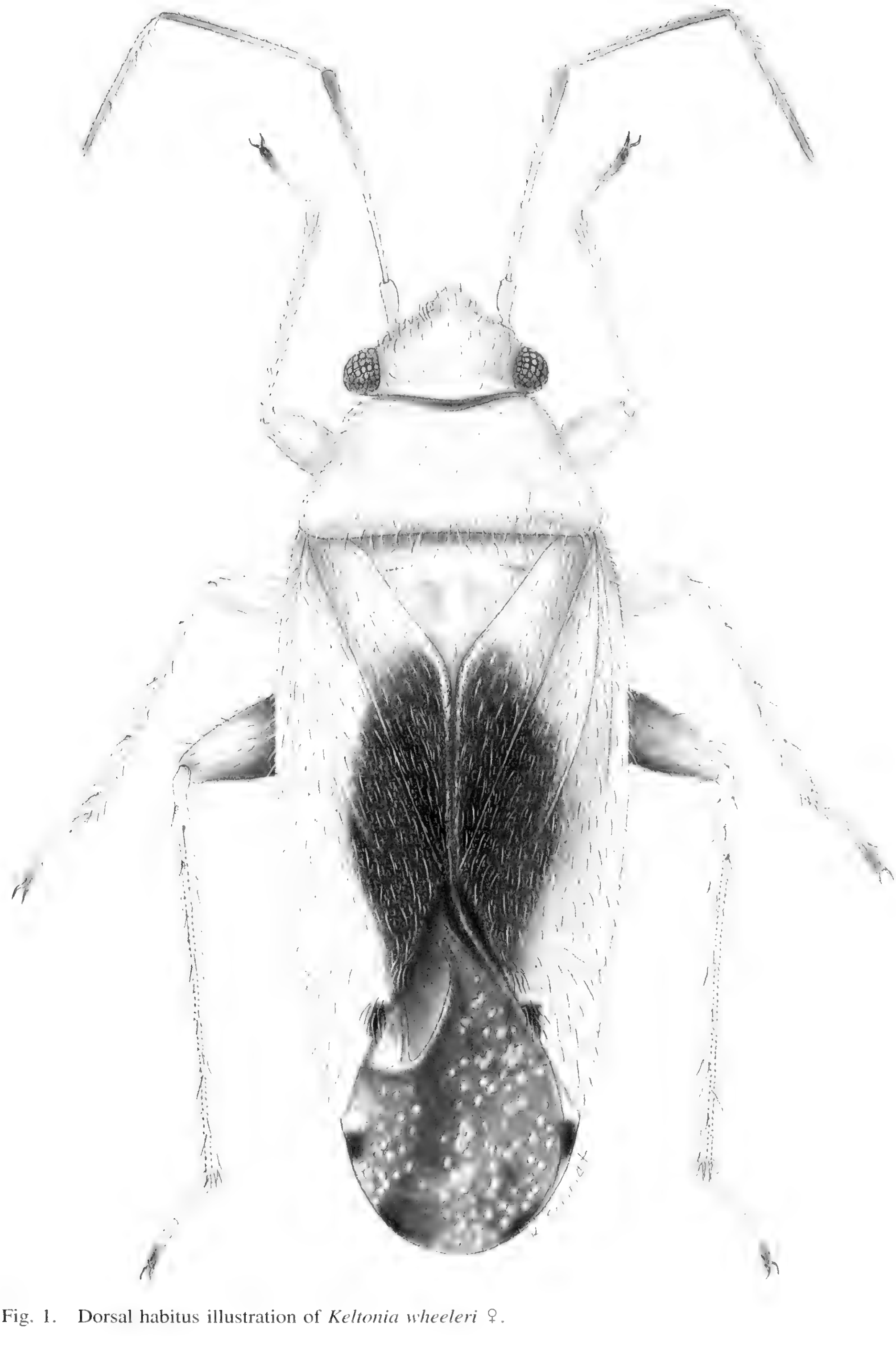
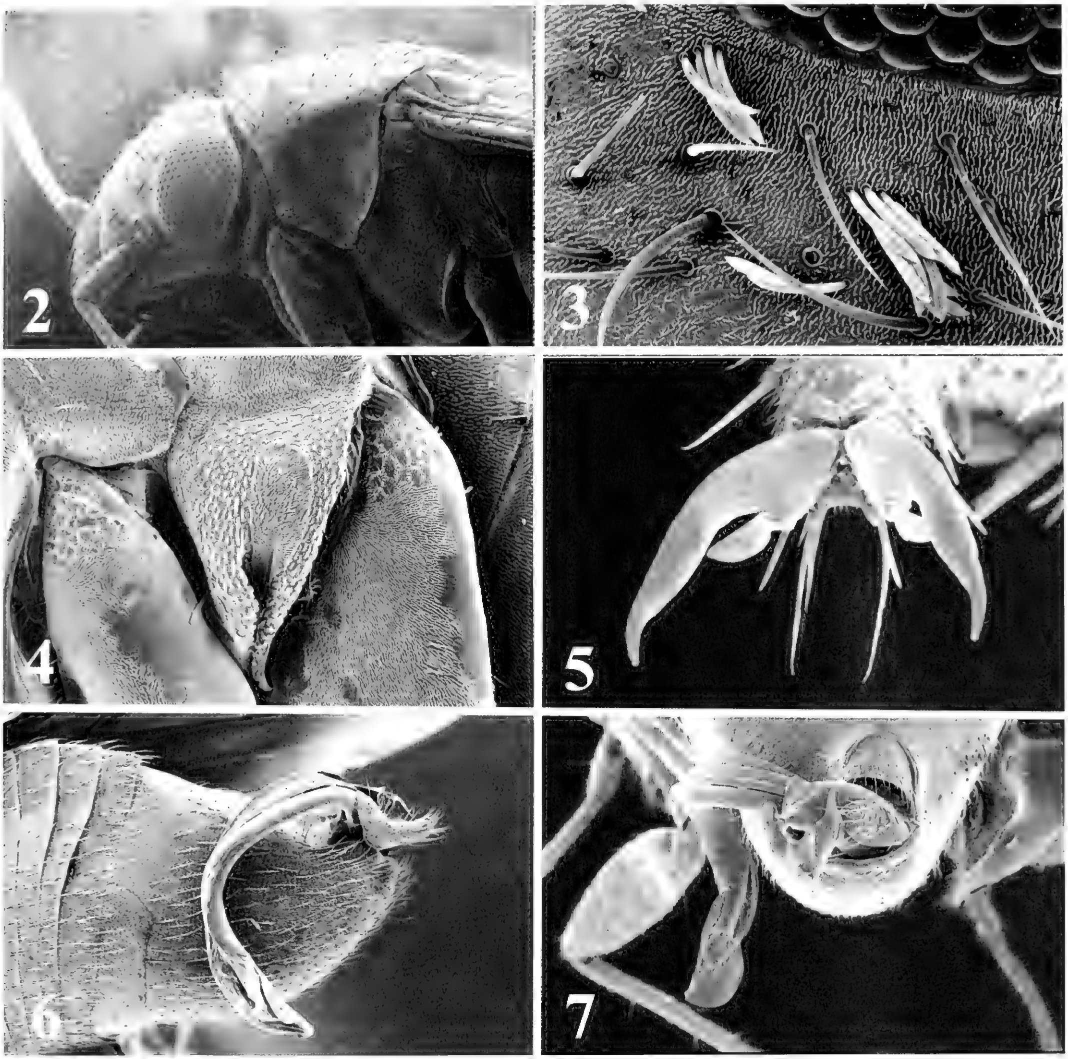


Fig. 1. Dorsal habitus illustration of *Keltonia wheeleri* ♀.



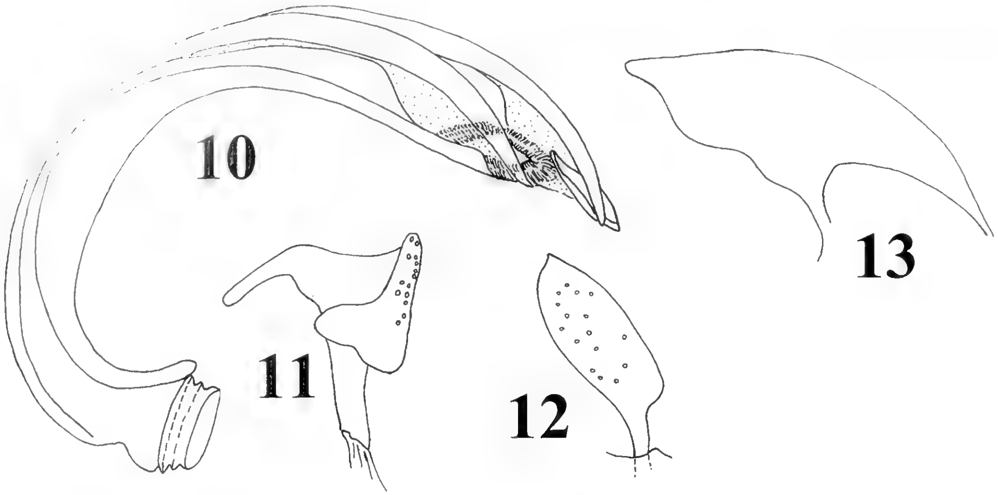
Figs. 2–7. Scanning electron micrographs of *Keltonia wheeleri*, ♂. 2, Head and pronotum, lateral aspect (122×). 3, Clusters of scalelike setae bordering compound eye (805×). 4, Metathoracic scent gland auricle and evaporatory area (326×). 5, Claw (1,170×). 6, Lateral aspect of genital capsule, with vesica extended (114×). 7, Caudal aspect of genital capsule, with vesica extended (118×).

(USNM); 5 ♂, 3 ♀, Jefferson Co., Rt. 1, 3.5 mi NE of Wrens, 1 July 1998, AGW, on *P. americana* (USNM); 13 ♂, 17 ♀, McDuffie Co., Rt. 221, 5 mi. S of Harlem, 11 Oct. 1998, AGW, on *P. americana* (AMNH, CNC, USNM, and TAMU); 2 ♂, 5 ♀, McDuffie Co., CR [county road]-86, nr jct rts 78 & 278, W of Dearing, 5 July 1998, AGW, on *P. americana* (USNM); 5 ♂, 2 ♀, Richmond Co., Rt. 1, Blythe, 1 July 1998, A. G. Wheeler, Jr. [AGW], taken on *P. americana* (USNM); 4 ♂, 6 ♀, Richmond Co., Wheeler Rd., Augusta, 1 July 1998, AGW, on *P. americana* (USNM); 4 ♂, 5 ♀, Richmond Co., Augusta, 18 Oct. 1998, AGW, on *P. americana* (USNM). SOUTH CAROLINA: 7 ♂, 32 ♀, same data as for holotype (AMNH, CNC, USNM); 1 ♂, 6 ♀, same data as for holotype, except taken on 5 June 1998 (USNM); 3 ♀, Aiken Co., Rt. 1 and CR-151, W. of Monetta, 28 June 1998, A. G. Wheeler, Jr.

Figs. 8, 9. Dorsal photographs of *Keltonia* spp. 8, *K. wheeleri*, ♂. 9, *K. rubrofemorata*, ♂.

coll., on *P. americana* (USNM); 1 ♂, 7 ♀, Aiken Co., Rt. 125, 1.7 mi. SE of Beech Island, 5 July 1998, AGW, on *P. americana* (USNM); 4 ♂, Aiken Co., Rt. 20w, exit 33, NW of New Holland, 28 June 1998, AGW, on *P. americana* (USNM); 2 ♀, Aiken Co., CR-1121, nr. Rt. 39, 4 mi. W of Wagener, 28 June 1998, AGW, on *P. americana* (USNM); 2 ♂, 5 ♀, Aiken Co., Rt. 19, 1 mi. S of Eureka, 18 Oct. 1998, AGW, on *P. americana* (USNM); 2 ♂, 5 ♀, Barnwell Co., Rt. 39, 0.2 mi. N of Rt. 278, SW of Williston, 18 Oct. 1998, AGW, on *P. americana* (USNM); 1 ♂, 2 ♀, Edgefield Co., Bettis Acad. Rd., 4.5 mi. SSW of Trenton, 5 June 1998, AGW, on *P. americana* (USNM); 1 ♂, 1 ♀, Edgefield Co., S-429 at junc Rt 25, 5.5 mi. N. of Augusta, 5 July 1998, AGW, on *P. americana* (USNM); 1 ♀, Edgefield Co., Rt. 25, 6.5 mi. N of Aiken Co. line, S of Trenton, 28 Nov. 1998, AGW, on *P. americana* (USNM); 4 ♂, 8 ♀, Edgefield Co., Mt. Zion Rd., NE of North Augusta, 5 June 1998, AGW, on *P. americana* (USNM); 5 ♂, 6 ♀, Lexington Co., CR-445, E of Rt. 178, SE of Batesburg, 28 June 1998, AGW, on *P. americana* (USNM); 2 ♀, Lexington Co., Rt. 178, 0.3 mi E of Rt. 20, N of Steedman, 28 June 1998, AGW, on *P. americana* (USNM); 8 ♂, 7 ♀, Orange Co., CR-1609, E of Rt. 39, 2 mi. SE of Salley, 28 June 1998, AGW, on *P. americana* (USNM, TAMU).

Discussion.—*Keltonia wheeleri* (Figs. 1, 8) is one of the more distinct species of the genus in having a bright, shiny yellow, dorsal coloration, with a large, dark, centrally located mark through the middle of the corium and across the apex of the clavus. It is most closely related to *K. rubrofemorata* (Fig. 9), the type of the genus, based on the overall coloration, male genital structures, and the unusual shared host genus (*Polygonella* Michx. [Polygonaceae]). *Keltonia wheeleri* has the head, all antennal segments, and the pro- and mesofemora yellowish, with only the apex of the metafemur tinged with pale red or orange, has a shorter antennal segment II (0.58–0.66 mm in ♂; 0.64–0.67 mm in ♀), has a larger hemelytral spot (Figs. 1, 8), and is found only on *Polygonella americana,* whereas *K. rubrofemorata* has the head, first antennal segment (and often segments II–IV), and all femora dark red, has a proportionately longer antennal segment II (0.68–0.70 mm in ♂, 0.68–0.76 mm in ♀), has a smaller he-



Figs. 10–13. Male genitalia of *Keltonia wheeleri*. 10, Vesica. 11, Left paramere. 12, Right paramere. 13, Phallotheca.

melytral spot (Fig. 9), and is found only on *P. myriophylla* (Small) Horton.

Couplet 2 of my key to the species of the genus (Henry 1991) may be modified as follows to accommodate *K. wheeleri*:

2a. Dorsum bright, shiny yellow; hemelytra lacking small brown spots or speckles surrounding brown cloud or solid dark area at middle; metafemur dark red or tinged with orange or red apically 2b
– Dorsum dull, sometimes phosphorescent yellow; hemelytra with numerous small spots or speckles surrounding brown cloud or dark area at middle; femora pale yellow to greenish yellow, never tinged with orange or red 3
2b. Head, antennal segment I, and all femora dark red (Fig. 9) . . . . *K. rubrofemorata* Knight
– Head, antennal segment I, and pro- and mesofemora pale yellow (Figs. 1, 8); metafemur tinged with orange or red only on apical ⅓ . . . . *K. wheeleri*, n. sp.

Pseudatomoscelis nubila Henry, new species

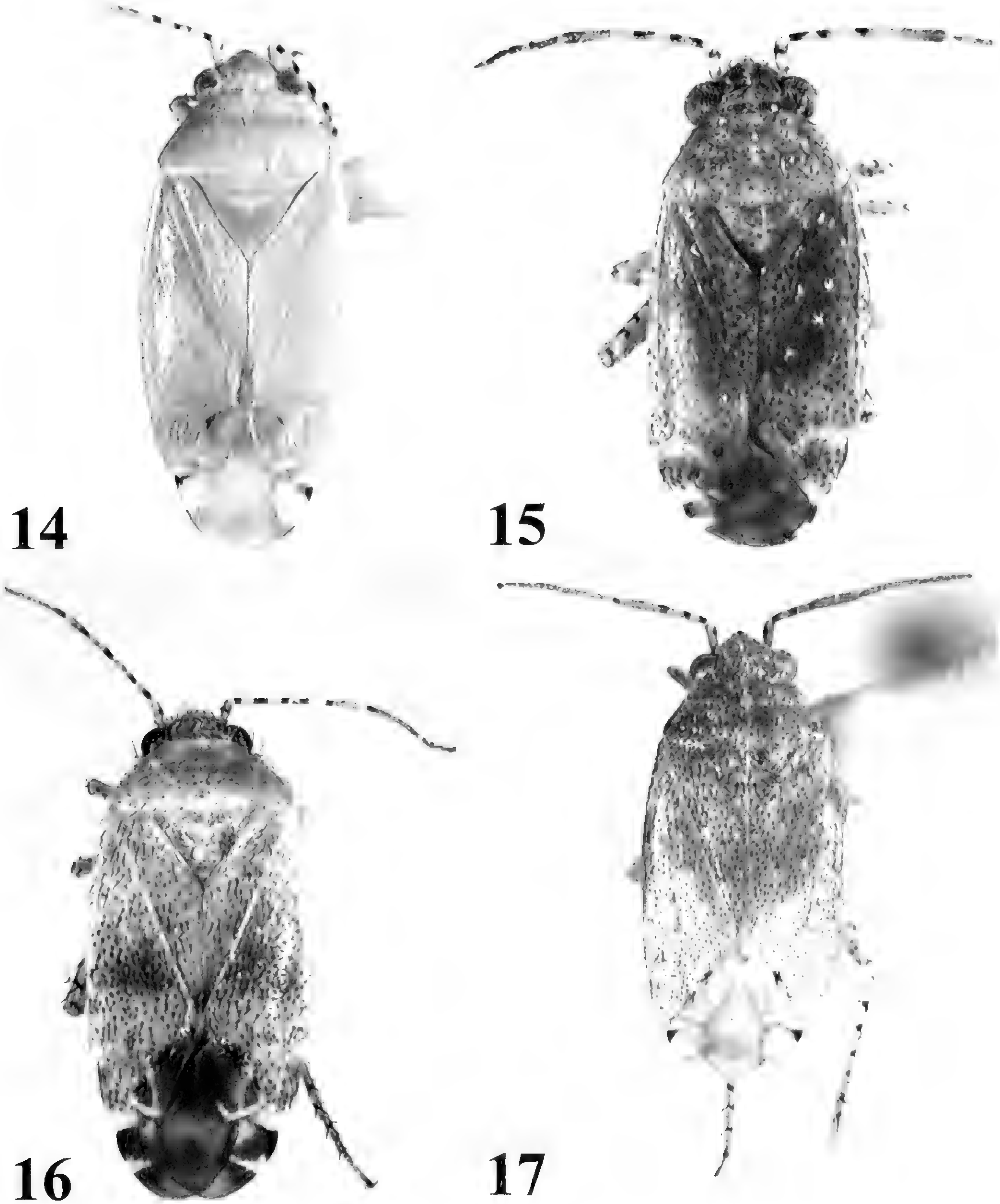
(Figs. 16, 18–21)

Diagnosis.—*Pseudatomoscelis nubila* (Fig. 16) is distinguished from all other species of the genus by the uniformly brown-spotted, yellow to greenish-yellow dorsum, with an irregular, transverse, brown band across the middle of the corium, and the mostly fuscous to black hemelytral membrane, having a pale or white spot near the apex of the cuneus and a narrower spot just beyond first spot.

Description.—*Male* (n = 10): Length 2.48–2.72 mm, width 1.13–1.16 mm. *Head:* Width 0.64–0.66 mm, vertex 0.29–0.30 mm. *Rostrum:* Length 1.06–1.12 mm, extending to middle of abdomen. *Antenna:* Segment I, length 0.18–0.20 mm; II, 0.67–0.77 mm; III, 0.40–0.43 mm; IV, 0.33–0.35 mm. *Pronotum:* Length 0.50–0.53 mm, basal width 0.96–1.16 mm.

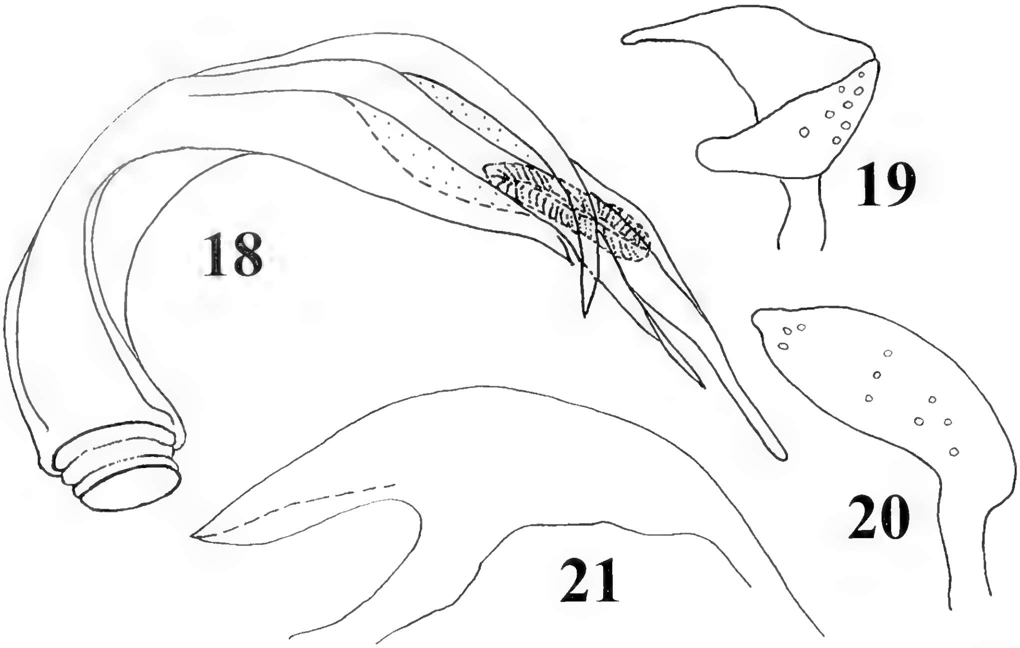
Female (n = 10): Length 2.56–2.80 mm, width 1.20–1.24 mm. *Head:* Width 0.60–0.62 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.02–1.14 mm, extending to base of ovipositor. *Antenna:* Segment I, length 0.20–0.21 mm; II, 0.65–0.77 mm; III, 0.36–0.38 mm; IV, 0.29–0.30 mm. *Pronotum:* Length 0.48–0.49 mm, basal width 0.98–1.02 mm.

Overall coloration golden yellow, evenly brown spotted on pronotum and hemelytra. Head golden yellow, paler along median line, with scattered brown or fuscous spots, mostly along inner margins of eyes and across base of vertex. Antenna yellow; seg-



Figs. 14–17. Dorsal photographs of *Pseudatomoscelis* spp. 14, *P. flora*, ♀. 15, *P. insularis*, ♂. 16, *P. nubila*, ♀. 17, *P. seriata*, ♂.

ment I with a partial to complete subapical and subbasal black band; segment II yellow, with four or five distinct black spots; segment III yellow to yellowish brown, narrowly fuscous at base; segment IV brown, narrowly black at base. Pronotum evenly brown spotted, less so on anterior ⅓ across calli; mesoscutum and scutellum evenly brown spotted. Hemelytron evenly brown spotted, with spots coalescing to form an



Figs. 18–21. Male genitalia of *Pseudatomoscelis nubila*. 18, Vesica. 19, Left paramere. 20, Right paramere. 21, Phallotheca.

irregular band across middle of corium; membrane fuscous or black, with two pale spots, one near apex of cuneus and a second narrower one just beyond first spot, sometimes slightly paler between areoles; veins yellowish, becoming fuscous on basal half or more of large areole. Ventral surface pale yellow, with a few scattered spots on abdomen; pleural area of pronotum often with an orange tinge or dash just above proacetabula. Legs yellow; coxae with a few scattered brown spots; femora evenly brown spotted; tibiae with large fuscous spots at bases of black spines; tarsi yellow; claws brown. Vestiture of two types: simple, erect, black setae arising from dorsal spots, black setae on head considerably longer than those on pronotum and hemelytra; and scattered clusters containing three to nine silvery, sericeus or scalelike setae on pronotum, scutellum, hemelytra, and along inner margin of eyes and across vertex of head.

Male genitalia: Vesica (Fig. 18); left paramere (Fig. 19); right paramere (Fig. 20); phallotheca (Fig. 21).

Etymology.—The specific name is from the Latin "nubila," meaning cloud, to draw attention to the mottled brownish band or cloud across the middle of the corium.

Host.—This species was collected on a shrublike species of *Croton* (Euphorbiaceae) growing in an arid habitat, containing native cacti, along the coast near Cabo Rojo, Dominican Republic.

Distribution.—Known only from southwestern Dominican Republic (Pedernales).

Type material.—Holotype ♂, Dominican Republic, Prov. Pedernales, 5 km N Cabo Rojo, nr sea level, 17°57′59″N 17°39′02″W, 12 April 2000, T. J. Henry & R. E. Woodruff, taken on *Croton* sp. (USNM). Paratypes: 17 ♂, 11 ♀, same data as for holotype (1 ♂, 1♀, AMNH; 1 ♂, 1 ♀ CNC; 15 ♂, 9 ♀ USNM).

Discussion.—This new species is most similar to *P. insularis* Henry (Fig. 15) and *P. seriata* (Reuter) (Fig. 17) in the overall brown-spotted dorsum. From *P. seriata,* it can be distinguished by the transverse brown band on the corium and the fuscous membrane and the stouter, more curved vesica (Fig. 18), having more pronounced spiculi. From *P. insularis*, it can be separated by the larger size, transverse corial band, and shape of the vesica. All of the above brown-spotted species are distinct from the uniformly yellowish-orange *P. flora* (Van Duzee) (Fig. 14), which lacks dorsal spots.

KEY TO SPECIES OF *PSEUDATOMOSCELIS*

1. Dorsum immaculate, without spots (Fig. 14); body yellow to yellowish orange; Arizona and Mexico . . . . *flora* (Van Duzee)
– Dorsum always with dark spots; body pale yellow to dark green, sometimes tinged with yellowish orange 2
2. Inner margin of cuneus without or with only vague spots bearing 2 or 3 bristlelike setae (Fig. 15); vesica of male short and stout; Puerto Rico and St. Thomas, West Indies . . . . *insularis* Henry
– Inner margin of cuneus with 1 or 2 distinct dark spots bearing numerous dark bristlelike setae; vesica of male more slender 3
3. Dorsum uniformly brown spotted (Fig. 17); hemelytral membrane mostly hyaline, often tinged with brown basally and with only a black dash just beyond apex of cuneus; widespread from Saskatchewan, Canada, to Venezuela, and the West Indies . . . . . *seriata* (Reuter)
– Dorsum uniformly brown spotted, but also usually with an irregular brown band across middle of corium (Fig. 16); hemelytral membrane mostly fuscous or black, with two pale areas, one just beyond apex of cuneus and a second more narrow one slightly beyond the first; Dominican Republic . . . . *nubila*, n. sp.

ACKNOWLEDGMENTS

I am grateful to A. G. Wheeler, Jr. (Department of Entomology, Clemson University, Clemson, SC) for providing me with the specimens of the interesting new species of *Keltonia* and R. E. Woodruff (Gainesville, Florida) for inviting me to join him on a productive, month-long collecting expedition to the Dominican Republic that yielded numerous interesting and several new species of Heteroptera, including *Pseudatomoscelis nubila*. I also thank Kathleen Schmidt (Hillsdale, New York) for the adult habitus illustration of *K. wheeleri* and Michele Touchet (Systematic Entomology Laboratory [SEL], ARS, USDA, % USNM) for the dorsal photographs used in this paper. M. G. Pogue (SEL), D. R. Smith (SEL), and A. G. Wheeler, Jr. kindly reviewed the manuscript and offered useful comments.

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NEW SPECIES OF *NOTHOTRICHIA* FLINT (TRICHOPTERA: HYDROPTILIDAE) FROM BRAZIL AND COSTA RICA

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Abstract.—The genus *Nothotrichia* was thought to be amphitropical in distribution. Two species, *N. cautinensis* Flint and *N. illiesi* Flint, are known from Chile and a third, *N. shasta* Harris and Armitage was described from California in the United States. The addition of two new species, ***N. tupi,*** from Brazil, and ***N. munozi,*** from Costa Rica, indicates that the genus occurs sporadically across the Neotropics.

Key Words: Trichoptera, Brazil, Costa Rica, new species, *Nothotrichia,* microcaddisfly, distribution

Flint (1967) erected the genus *Nothotrichia* for the Chilean species *N. illiesi.* A second species from Chile, *N. cautinensis* Flint, was added in 1983 (Flint 1983). The genus was thought to be endemic to the Chilean subregion until a third species, *N. shasta* Harris and Armitage, was discovered in North America from northern California. It was suggested that the genus displayed an amphitropical distribution (Harris and Armitage 1997). The discovery of two additional new species from Brazil and Costa Rica, collected as part of ongoing inventories of the caddisfly faunas of those countries, expands the distribution of the genus substantially. *Nothotrichia* are infrequently collected and specimens within collections are few, thus the genus may occur in intervening areas.

Specimens are deposited in the collections of the Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP), the University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH).

Nothotrichia munozi Holzenthal and Harris, new species

(Fig. 1)

This new species shares with its congeners features of the head and thorax typical for the genus (Harris and Armitage 1997). Although quite different in many details of the male genitalia, this species is more closely aligned with *N. cautinensis* Flint and *N. shasta* Harris and Armitage than with *N. illiesi* Flint. With *N. cautinensis, N. munozi* shares the feature of long narrow processes from the dorsum of segment IX; and with *N. shasta,* the elongate process from the base of the inferior appendage. The new species is immediately distinguished by the longer inferior appendage, which also has a large dorsal spine at midlength and a very long inner process from the base.

Male.—Length 2.3 mm. Antenna simple with 25 segments. Preserved in alcohol with no evident pattern to the wings. Abdominal segment VII with short ventromesal process. Segment VIII annular, dorsum slightly wider than venter. Segment IX

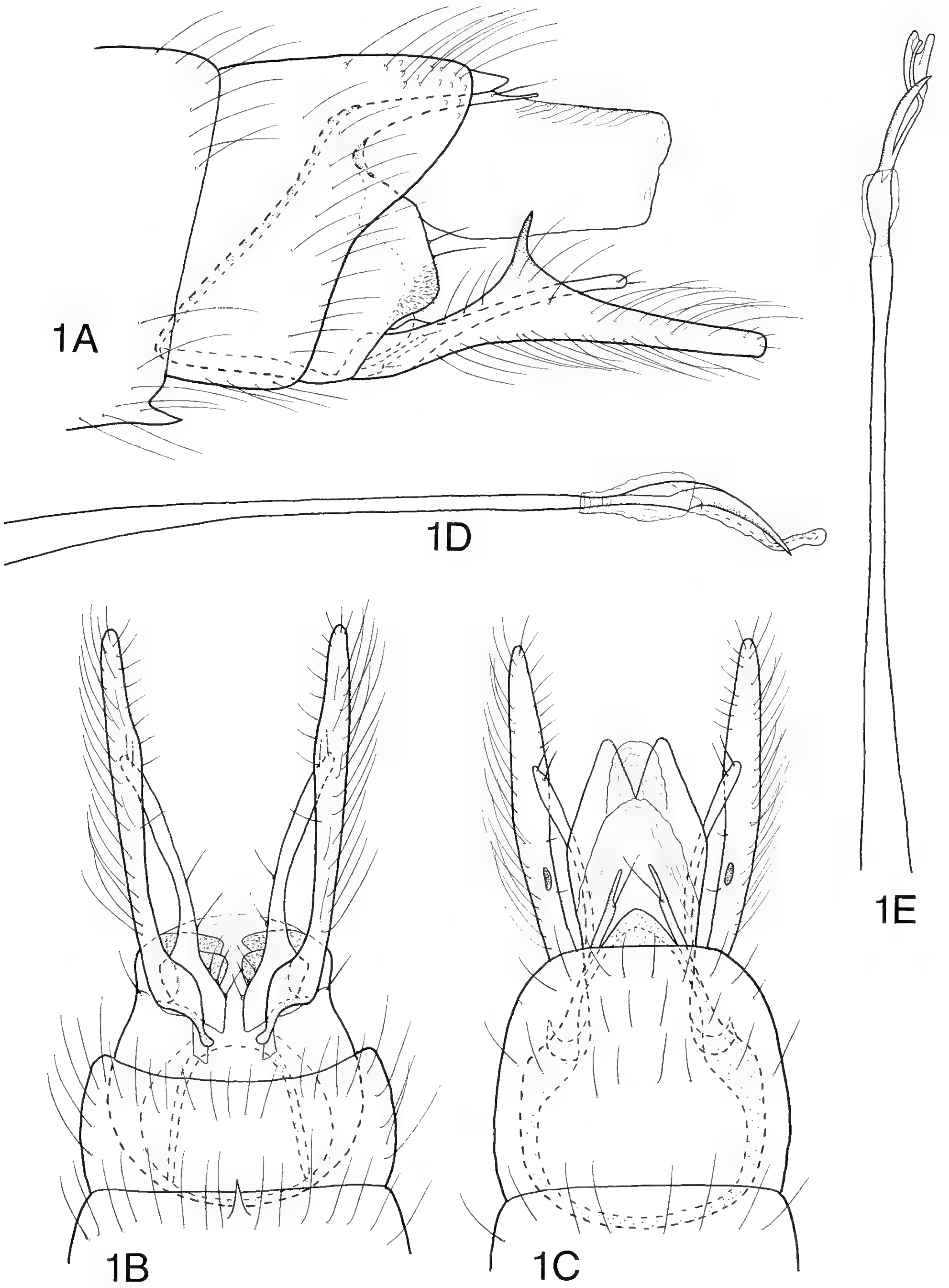

Fig. 1. *Nothotrichia munozi,* ♂ genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

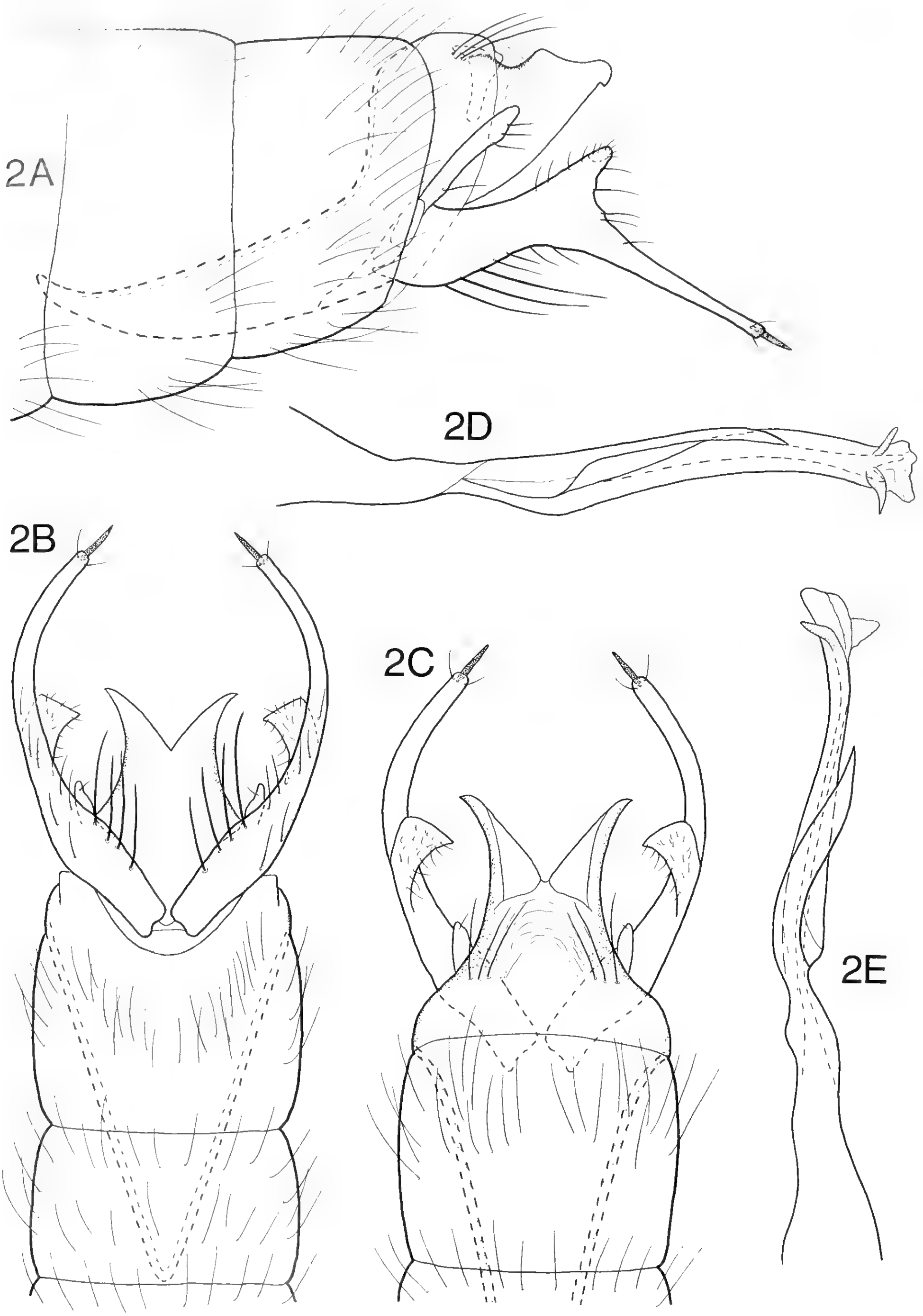

Fig. 2. *Nothotrichia tupi*, ♂ genitalia. A, Lateral. B, Ventral. C, Dorsal. D, Phallus, lateral. E, Phallus, dorsal.

largely enclosed within VIII, in lateral view narrowing dorsally, with elongate thin processes extending posteriorly, posteroventrally with setose lobe; in dorsal and ventral views, rounded anteriorly; ventrally with posterior setose lobe divided mesally. Segment X elongate and rectanguloid in lateral view; dorsally a narrow membranous lobe, incised distally. Inferior appendages thin and elongate in lateral view, heavy sclerotized spinose process at midlength extending dorsad; in ventral view narrow over length, thin processes originating mesally at base and extending beyond midlength, apex tipped with pair of setae. Phallus thin and tubular, apex divided into two processes, one sickle-shaped, the other tubular and bearing the ejaculatory duct.

Female.—Unknown

Type material.—Holotype, ♂. COSTA RICA: Guanacaste: Area de Conservación Guanacaste, Parque Nacional Guanacaste, Estación Maritza, Río Tempisquito, 10.958°N, 85.497°W, el. 550 m, February 1994, Fdo. Muñoz-Q (UMSP).

Etymology.—Named for Fernando Muñoz, who collected the specimen and contributed much to our knowledge of the Costa Rican caddisfly fauna.

Nothotrichia tupi Holzenthal and Harris, new species

(Fig. 2)

In overall appearance of the genitalic structures, particularly the inferior appendages, this new species is very similar to *N. munozi.* Both have elongate inferior appendages, with a dorsal process arising near midlength, which is spinose in *N. munozi* and rounded in the new species, and both have an elongate process originating at the base of the appendages. The new species lacks the narrow dorsal processes from segment IX, seen in both *N. munozi* and *N. cautinensis,* and as well segment X tapers distally in the new species, similar to that seen in *N. cautinensis* and *N. shasta,* as opposed to the truncate distal shape seen in *N. munozi.*

Male.—Length 2.4–2.7 mm. Antenna simple with 25 segments. Brown in color with diffuse silver hairs on forewing and patches of silver hair on thorax and head. Abdominal segment VII annular, lacking ventromesal process. Segment VIII annular, posterior margin emarginate ventrally. Segment IX largely enclosed within segments VII and VIII, in lateral view narrowing dorsally and tapering anteriorly; in dorsal view triangular, and seemingly fused with X posteriorly, series of setae posterolaterally. Segment X short in lateral view, tapering distally to knob-like apex, anteriorly with elongate sclerite within segment IX; dorsum divided posteriorly with sclerous lateral margins, anteriorly with sclerotized bands laterally at juncture with segment IX. Inferior appendages thin and elongate in lateral view, tipped apically with stout spine, rounded dorsal process near midlength, elongate process originating at base and extending dorsad; in ventral view thin over length and curving inward, basal process appearing to be short, midlength process squarish. Phallus tubular with ribbon-like sheath originating near midlength, apex bearing pair of short lateral processes, one of which is associated with the ejaculatory duct.

Female.—Unknown.

Type material.—Holotype, ♂. BRAZIL: Minas Gerais: Parque Estadual Itacolomi, Rio Belchior, 20°25.041′S, 43°25.633′W, el. 725 m, 2.ii.1998, Holzenthal & Paprocki (MZUSP). Paratypes: Same data as holotype, 1 ♂ (UMSP), 1 ♂ (NMNH).

Etymology.—Named for the Tupi-Guarani, the indigenous people of southeastern Brazil.

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A NEW GENUS AND A NEW SPECIES OF DALADERINI (HEMIPTERA: HETEROPTERA: COREIDAE) FROM MADAGASCAR

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Abstract.—***Kerzhnercryptes perinetus*, n. gen., n. sp.**, from Madagascar are described in the tribe Daladerini (Coreidae). A habitus view illustration and drawings of the antennae, pronotum, legs, abdomen, and male and female genitalia are provided. A key to the known genera of Daladerini from Madagascar is included.

Key Words: Insecta, Heteroptera, Coreidae, Daladerini, new genus, new species, Madagascar

The Coreidae fauna of Madagascar is rich and diverse but has been studied little by modern workers. The tribe Daladerini at present is composed of 8 genera and 28 nominal species distributed throughout the Old World tropics, with the majority of species and the greatest diversity in southern Africa.

The Madagascar Daladerini have never been revised. The first species recorded was by Stål (1873), who described a new genus and one new species, *Odontorhopala callosa.* Distant (1879) studied the Madagascar Hemiptera and added one new genus, *Parabrachytes,* with two new species, *P. coloratus* and *P. obscurus,* and later Distant (1893) described *Odontorhopala bergrothi* and discussed the generic position of *Odontorhopala* and *Parabrachytes.* Bergroth (1906) described a new genus and one new species, *Rhombolaparus tardigradus,* and later Bergroth (1912) added the new species, *Odontorhopala geminata.* Garcia Varela (1913) described *Parabrachytes longicornis* and gave new distribution records for *Odontorhopala callosa* and *Parabrachytes coloratus.*

Here I add a new genus and a new species in order to make the name available for discussion of the zoogeography of the tribe.

The following abbreviations are used for the institutions cited in this paper: MNHN (Muséum National d'Histoire Naturelle, Paris, France), UNAM (Instituto de Biología, Universidad Nacional Autónoma de México), ZISP (Zoological Institute, St. Petersburg, Russia).

All measurements are given in millimeters.

CHECKLIST OF THE GENERA AND SPECIES OF MADAGASCAR DALADERINI

Kerzhnercryptes Brailovsky, new genus.
    K. perinetus Brailovsky, new species.
Odontorhopala Stål 1873: 55–56.
    O. bergrothi Distant 1893: 54.
    O. callosa Stål 1873: 56.
    O. geminata Bergroth 1912: 82–83.
Parabrachytes Distant 1879: 213–214.
    P. coloratus Distant 1879: 214.
    P. longicornis Garcia Varela 1913: 20–21.
    P. obscurus Distant 1879: 214–215.
Rhombolaparus Bergroth 1906: 17–18.
    R. tardigradus Bergroth 1906: 18.

Kerzhnercryptes Brailovsky, new genus

Diagnosis.—This genus appears to be closely related to *Parabrachytes* Distant (1879) particularly due to the relatively narrow, non-expanded abdomen (Fig. 9), and the humeral angles of the pronotum not conspicuously expanded as a wing-like lobes (Figs. 7–8). *Kerzhnercryptes* has antennal segment II almost cylindrical without distal spines (Fig. 1), the rostrum elongate, slender and reaching abdominal sternite III, each femur slender and armed ventrally with two small subapical spines (Fig. 16), the humeral angles of the pronotum subacute (Fig. 7), and the tibiae longer, and more slender. *Parabrachytes* is distinguished by having antennal segment II distally clavate and armed with strong spines (Fig. 3), the rostrum short, robust and not extending beyond the middle third of the mesosternum, the femora robust and ventrally armed with two rows of stout spines (Fig. 5), the humeral angles rounded, and obtuse (Fig. 8), and the tibiae short, and robust.

Rhombolaparus Bergroth (1906) is clearly distinguished by having the abdomen conspicuosly dilated, rhomboidal, and the humeral angles of pronotum laterally expanded.

Generic description.—Body medium sized to large, moderately elongate. *Head:* Across eyes wider than long, subquadrate, dorsally flat; tylus conspicuously deflexed, unarmed, apically truncated, and shorter than juga; juga produced forward on a strong conical tubercle, extending anteriorly to tylus and slightly raised in lateral view; vertex with deep longitudinal groove along midline; antenniferous tubercle large, prominently produced, wide, separated by distance equal to their own width; sides of head in front of eyes almost straight; antennal segment I slightly robust, thickest and much longer than head; segments II and III cylindrical, slender; segment IV fusiform; antennal segment I longest, II longer than III, IV the shortest (Fig. 1); ocelli scarcely tuberculate; preocellar pit deep, diagonally excavated; eyes protruding, hemispherical; postocular tubercle protuberant; buccula rounded, raised, short, not extending beyond antenniferous tubercle, with short spine anterior projection; rostrum reaching anterior third of abdominal sternite III; mandibular plate unarmed.

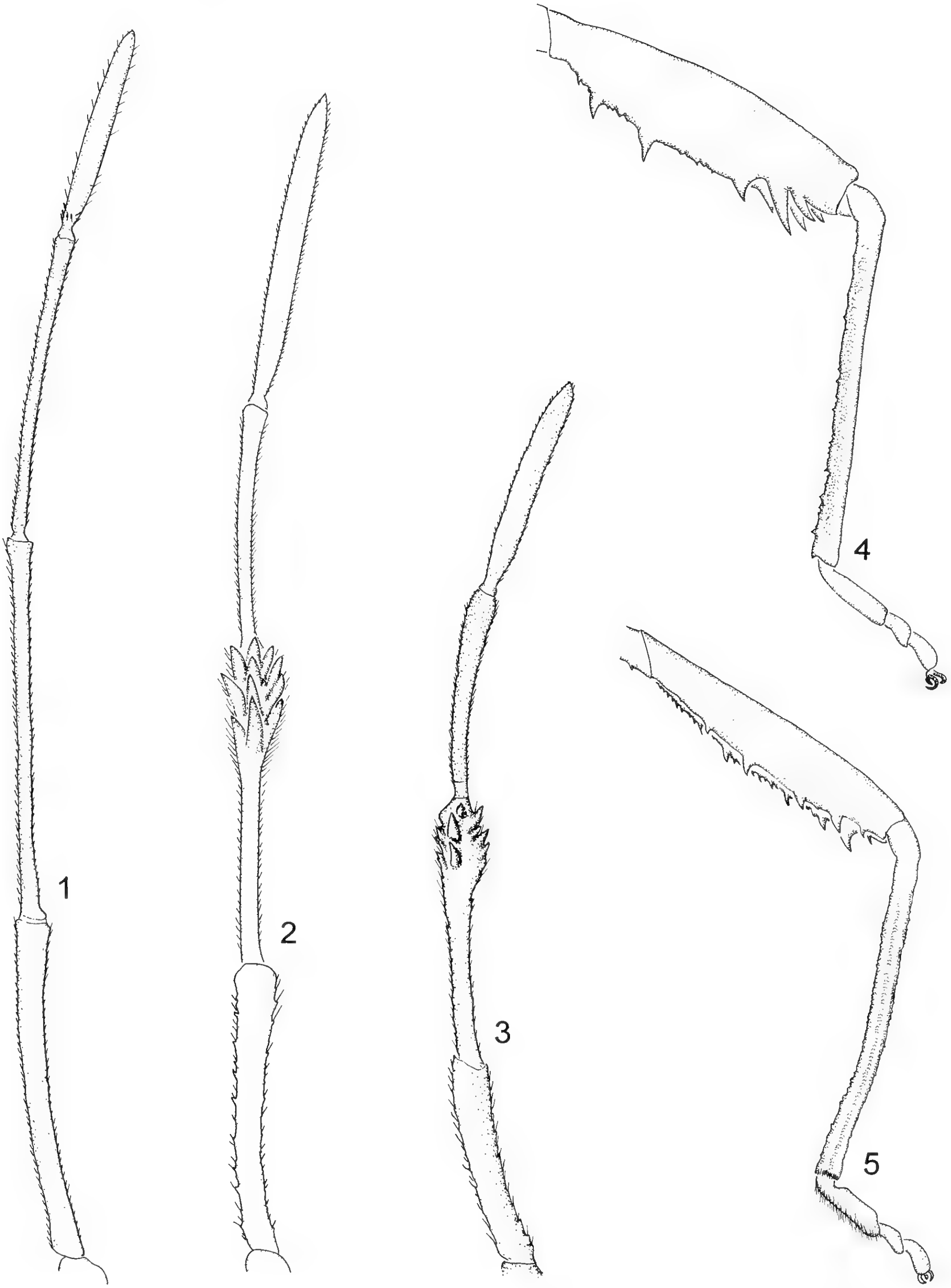
Thorax: Pronotum wider than long, trapeziform, moderately declivent; collar not distinctly marked; anterolateral margins obliquely straight, coarsely nodulose; frontal angles obtuse; humeral angles produced laterad, directed upward and each margin finely nodulose (Fig. 7); posterolateral margin sinuate, with upper half nodulose and inner half smooth; posterior margin smooth, concave; callar region indistinct, transversely flat, separated along midline by an obscure longitudinal groove; posterior margin with transverse ridge, distinctly raised; prosternum with deep excavation; mesosternum with a broad, medio-longitudinal groove; metasternum entire; anterior lobe of metathoracic peritreme elevated, reniform, posterior lobe sharp, small.

Legs: Femora slightly incrassate, surface smooth, armed with two small anteapical spines; tibiae cylindrical, sulcate, unarmed.

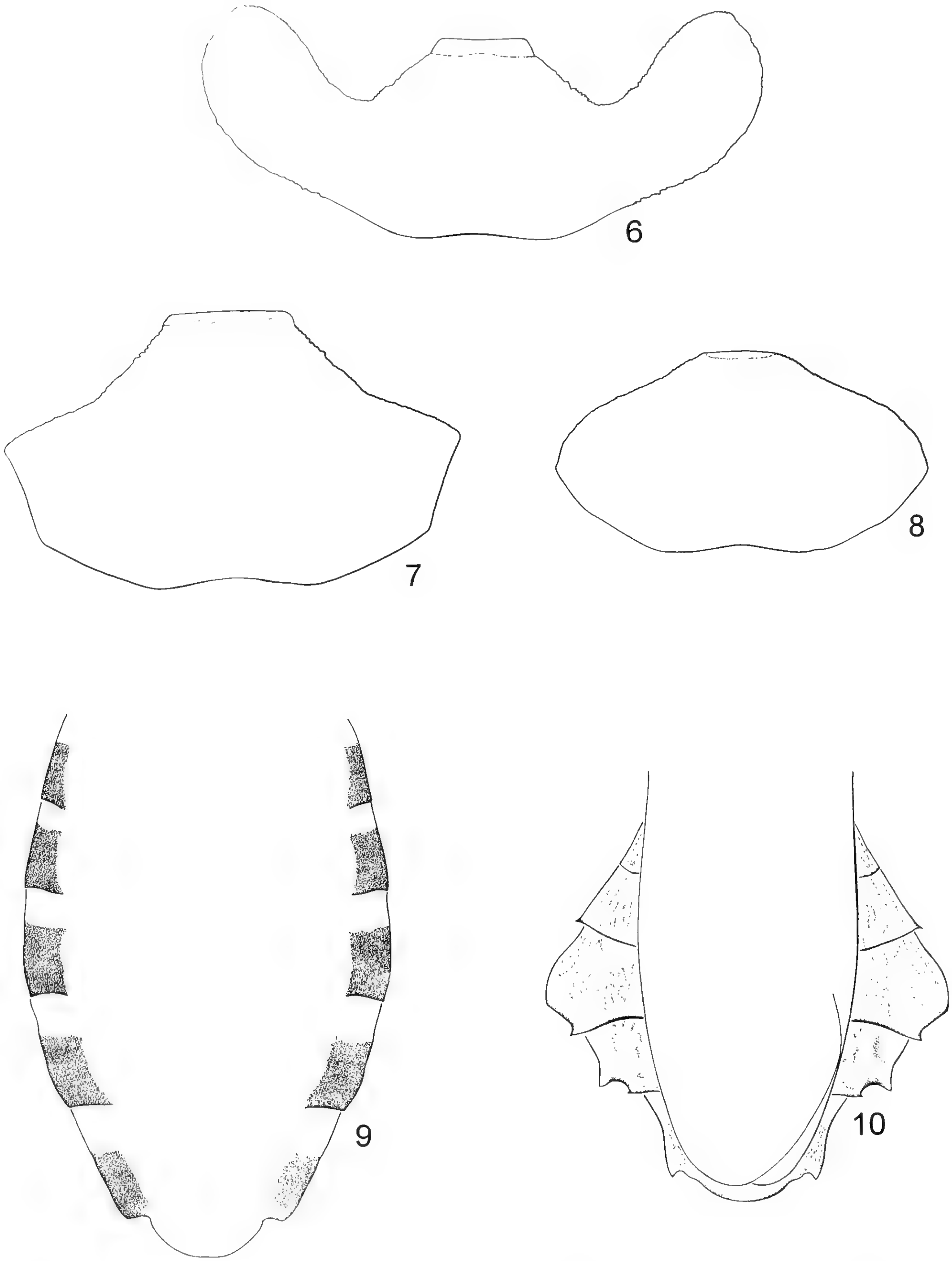
Scutellum: Triangular, flat, relation length-width, with two conditions independent of the sex, longer than wide, or wider than long, and transversely striated; apex short, acute.

Hemelytra: Macropterous, reaching apex of last abdominal segment; costal margin with a shallow groove; apical margin obliquely straight, with short apical angle almost reaching middle third of hemelytral membrane.

Abdomen: Connexival segments higher than margin of hemelytron at rest; upper margin smooth; posterior angles simple, not spinose; posterior third of connexival segments III, IV and VII straight, and posterior third of segments V and VI depressed, concave or diagonally truncated; abdominal spiracle closer to anterior margin than to posterior margin.



Figs. 1–5. 1–3, Antenna. 1, *Kerzhnercryptes perinetus*. 2, *Odontorhopala callosa*. 3, *Parabrachytes coloratus*. 4, 5, Hind leg. 4, *O. callosa*. 5, *P. coloratus*.



Figs. 6–10. 6–8, Pronotum. 6, *Odontorhopala callosa*. 7, *Kerzhnercryptes perinetus*. 8, *Parabrachytes coloratus*. 9, 10, Abdomen. 9, *K. perinetus*. 10, *O. callosa*.

Integument: Body surface rather dull, almost glabrous. Dorsal head, pronotum, scutellum, clavus, corium, propleura, mesopleura, metapleura, abdomen, and exposed parts of genital segments of both sexes punctate. Ventral head, calli, connexival segments, prosternum, mesosternum and metasternum impunctate; antenniferous tubercles granulate.

Male genitalia: Genital capsule: Posterior margin simple, convex (Fig. 13). Parameres: Shaft robust; anterior lobe convex, posterior lobe short and slender (Figs. 11–12).

Female genitalia: Abdominal sternite VII with plica and fissura; plica triangular, reaching anterior third of sternite VII; gonocoxae I enlarged dorso-ventrally, in caudal view closed, in lateral view convex, with upper margin rounded; paratergite VIII triangular, with spiracle visible but hard to see; paratergite IX squarish, larger than paratergite VIII (Fig. 15). Spermatheca: Distal bulb spherical; sclerotized duct leading from bulb moderately coiled; chamber elongate with acute lateral spines, distal duct straight and widely membranous duct (Fig. 14).

Etymology.—Named for I. M. Kerzhner distinguished Russian hemipterist.

Type species.—*Kerzhnercryptes perinetus,* new species.

Kerzhnercryptes perinetus Brailovsky, new species

(Figs. 1, 7, 9, 11–16)

Description.—Measurements: *Male:* Head length 2.00; width across eyes 2.23; interocular space 1.30; interocellar space 0.62; preocular distance 1.32; length antennal segments: I, 4.71; II, 4.96; III, 3.96; IV, 2.91. Pronotum: Total length 3.78; width across frontal angles 1.73; width across humeral angles 6.69. Scutellar length 2.31; width 2.29. Total length 21.10. *Female:* Head length 2.12; width across eyes 2.41; interocular space 1.50; interocellar space 0.65; preocular distance 1.44; length antennal segments: I, 5.08; II, 5.56; III, 4.46; IV, 3.10. Pronotum: Total length 4.34; width across frontal angles 1.98; width across humeral angles 7.87. Scutellar length 2.88; width 2.91. Total length 24.80.

Male coloration: Dorsal coloration: Head, pronotum, clavus and corium chestnut orange; scutellum yellow with apex chestnut orange and a black square at basal middle third; corium with black spots scattered along costal border; connexival segments black with anterior third or anterior half orange yellow; dorsal abdominal segments shining orange yellow; hemelytral membrane pale orange brown; antennal segment I yellow, II and III yellow with apical third black, and IV creamy yellow. Ventral coloration: Pale orange yellow with following areas black: apex of rostral segment IV, anterior and posterior lobe of metathoracic peritreme, 1 to 3 discoidal spots on coxae, dense discoidal spots on femora and tibiae and few scattered spots on abdominal sterna III to VII.

Female coloration: Similar to male. Dorsal abdominal segments VIII and IX and genital plates pale orange yellow.

Types.—Holotype: ♂, Madagascar, Analamasotra, Pr. Perinet, December 1930 (without collector) (ZISP). Paratypes: 3 ♂, 4 ♀, same data as holotype (UNAM, ZISP). 2 ♂, 2 ♀, Madagascar, Perinet, December 1932 (without collector) (ZISP). 6 ♂, 6 ♀, Madagascar, Dist. Mananara, N. Mont Antampona, July 1965, Vadon, Peyrieras (MNHN, UNAM).

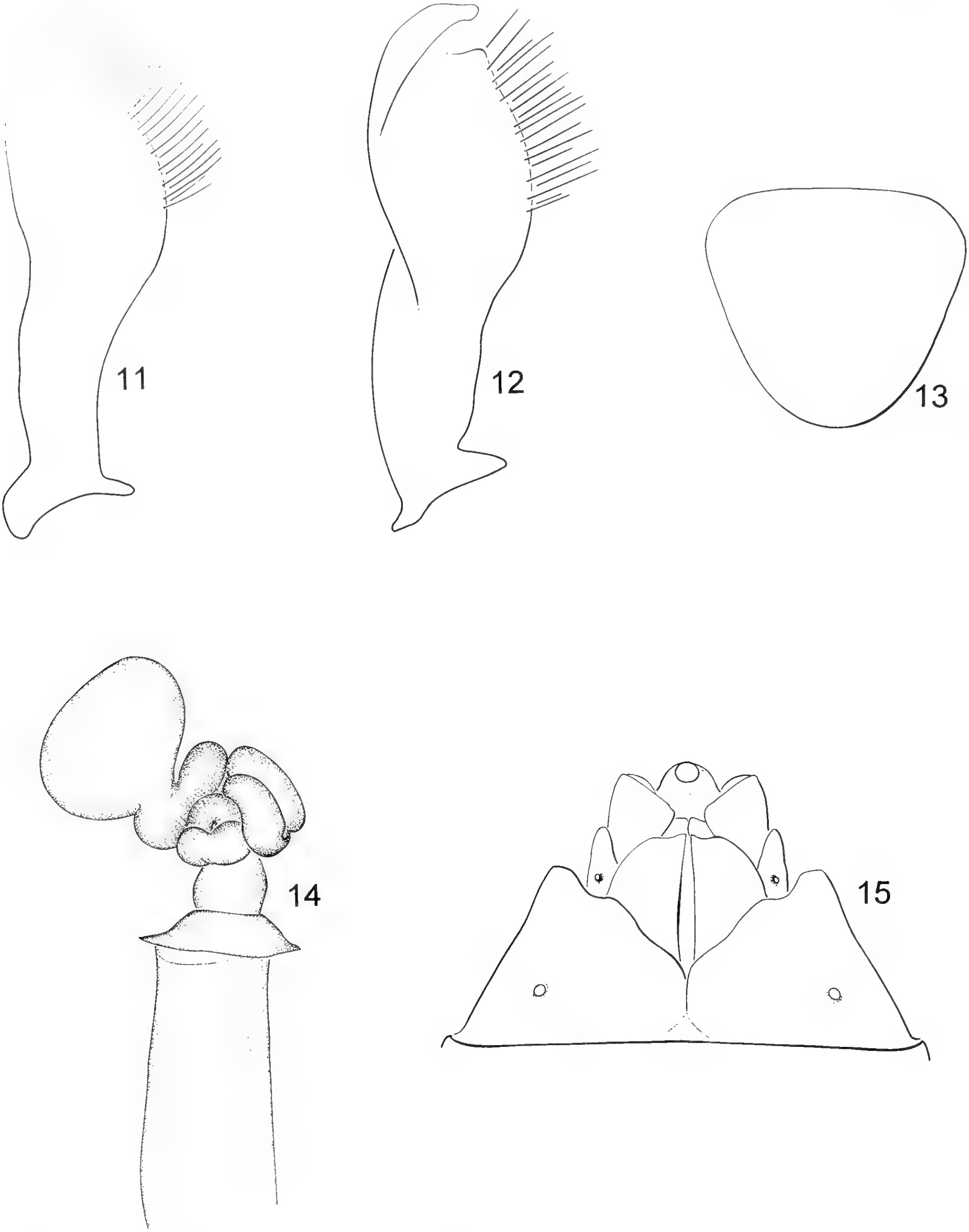
Etymology.—Named for the type locality; a noun in apposition.

Distribution.—Known only from Madagascar.

KEY TO THE KNOWN GENERA OF DALADERINI FROM MADAGASCAR

1. Antennal segment II clavate, with distal third armed with stout spines (Figs. 2–3); hind femur robust, ventrally armed with two rows of stout and large spines (Figs. 4–5) 2

– Antennal segment II almost cylindrical without distal spines (Fig. 1); hind femur elongate, slender, slightly thickened toward apex, and



Figs. 11–15. *Kerzhnercryptes perinetus*. 11, 12, Parameres. 13, Male genital capsule in caudal view. 14, Spermatheca. 15, Female genital plates.

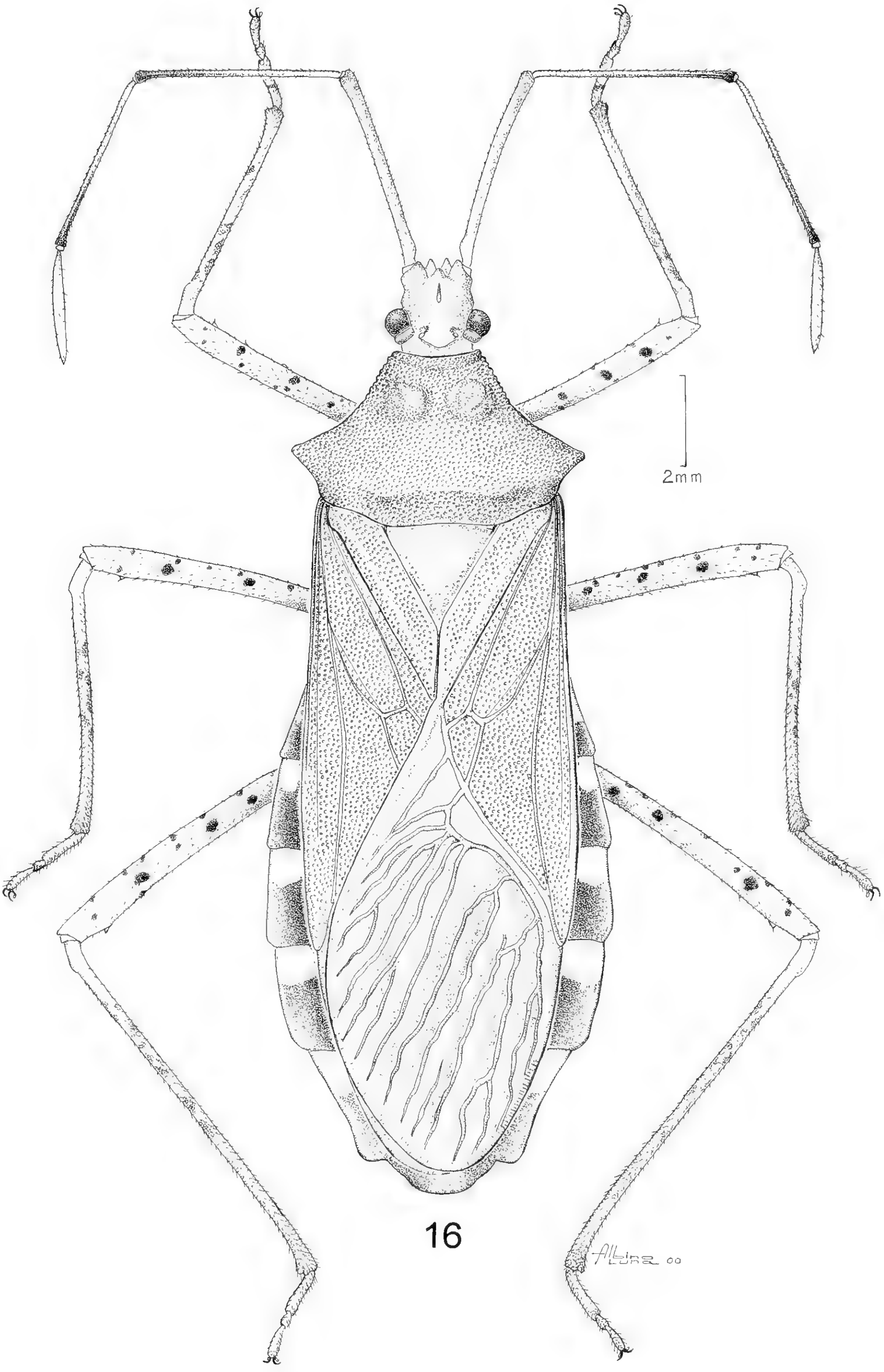


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Fig. 16. Dorsal view of *Kerzhnercryptes perinetus.*

ally with two minute or indistinct spines 3

eral angles obtuse, rounded, not expanded: abdominal segments not expanded laterally (Fig. 8) . . . . *Parabrachytes* Distant

Humeral angles strongly produced laterally and anteriorly into rounded wing-like lobes (Fig. 6); abdomen strongly and abruptly dilated (Fig. 10) . . . . *Odontorhopala* Stål

3. Abdomen strongly expanded in middle, rhomboidal in outline . . . . . *Rhombolaparus* Bergroth

– Abdomen not expanded, relatively narrow, parallel-sided (Fig. 9) . . . . *Kerzhnercryptes* Brailovsky, new genus

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A NEW SPECIES OF *GLYPHIDOCERA* WALSINGHAM (LEPIDOPTERA: GELECHIOIDEA: GLYPHIDOCERIDAE) FROM COSTA RICA

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Abstract.—***Glyphidocera guaroa*, n. sp.,** is described from Costa Rica. A photograph of the imago and illustrations of wing venation, male abdominal sex scales, and male and female genitalia are provided.

Key Words: Lepidoptera, Gelechioidea, Costa Rica, Puntarenas, Heredia, Guanacaste, Limón

Glyphidocera Walsingham (1892) are small to medium-sized moths that vary in color from pale yellowish brown to dark brown with few, if any, diagnostic markings. Limited to the New World, their greatest diversity is in the tropics where the numbers of species of *Glyphidocera* are about ten times greater than that of the temperate region. Host associations are unknown for all but *G. juniperella,* which feeds on *Juniperus horizontalis* Moench (Cupressaceae) (Adamski and Brown 1987).

Glyphidocera was first recognized by Walsingham (1892) who described *G. audax* from Saint Vincent Island in the West Indies. Originally placed the Gelechiidae (Walsingham 1892), *Glyphidocera* later was transferred (Hodges 1978), with several other genera, to the Symmocinae (Blastobasidae). Hodges later (1998) transferred Symmocinae to Autostichidae, except for *Glyphidocera,* which he elevated to family rank based on two apomorphies: 1) forewing with CuA_1 and CuA_2 stalked and downcurved from posterodistal angle of cell, and 2) forewing with Rs terminating on the outer margin. Becker (1999), following Hodges (1998), recognized two gelechiid genera, *Ptilostonychia* Walsingham and *Stibarenches* Meyrick, as junior synonyms of *Glyphidocera.*

Glyphidoceridae usually can be recognized by a combination of the following characters: male 4th flagellomere with tuft of setiform scales on dorsal surface extending over concavity with sex scales on the lateral surface of 5th and 6th flagellomeres; male abdomen with squamiform or piliform sex scales on intersegmental membrane between terga 2–3 and/or terga 3–4; valva narrowed basally, abruptly widened apically, apex protracted, base of costa with digitate process; sacculus twisted apically; gnathos projecting dorsally from beneath tuba analis, juxta basally narrow and fused to vinculum, distolaterally expanded and forming a ventral support for the aedeagus; aedeagus with medium to large cornutus or cornuti; ductus ejaculatoris spiralled; female ductus bursae large, sclerotized, with funnel-shaped antrum; ductus seminalis spiralled from middle or posterior end of corpus bursae and with internal sclerotized support; and corpus bursae spinulate, especially at anterior end, and with a sclero-

Fig. 1. Holotype of *Glyphidocera guaroa*.

tized plate opposite base of ductus seminalis.

Kornerup and Wanschner (1978) is used as a color standard for the description of the adult vestiture. Genitalia were dissected as described by Clarke (1941), except that mercurochrome and chlorazol black were used as stains. Measurements of wings and genitalia were made using a calibrated ocular micrometer.

The following species is described as part of several major studies planned by the author, including the *Glyphidocera* of Costa Rica.

Glyphidocera guaroa Adamski, new species
(Figs. 1–6)

Diagnosis.—*Glyphidocera guaroa* can be distinguished from other species of *Glyphidocera* by the following combination of characters: squamiform sex scales on the intersegmental membrane between abdominal terga 2–3 of the male, an elongate uncus, a bulbous gnathos; a widely bifurcate apex of valva, an aedeagus with a large cornutus; female antrum with long longitudinal ridges, and ductus seminalis spiralled, extremely wide basally.

Glyphidocera guaroa is most similar to *G. alexandrae* Adamski and Brown (2001) but differs from the latter species by having a bifurcate costal apex of the valva.

Description, adult.—*Head:* Vertex and frontoclypeus pale brownish orange intermixed with brown marginal scales tipped with pale brownish orange; outer surface of labial palpus brown intermixed with few pale brownish-orange scales, inner surface pale brownish orange intermixed with few brown scales; scape, pedicel and flagellomeres 1–6 brownish orange, flagellomeres brown distally; 4th flagellomere with a tuft of setiform scales on dorsal surface in male, extending over concavity on 5th and 6th flagellomeres; proboscis pale brownish orange.

Thorax: Mesonotum and tegula pale

brownish orange intermixed with few brown scales; legs pale brownish orange intermixed with brown scales; some specimens with areas at midsegment and apical areas of all segments and tarsomeres pale brown; forewing (Figs. 1–2) length 5.9–7.5 mm (n = 121), brownish orange intermixed with pale brownish-orange scales tipped with brown and few brown scales; costa and outer margin brown intermixed with few pale-brown scales; discal cell with two spots, one near middle and one near distal end; one brown spot or streak from base of CuP to near midcell spot (spots may be faint in rubbed specimens); fringe scales brown; venation (Fig. 2) with R_3, R_4, and R_5 approximate to distoanterior part of cell; M_2 and M_3 approximate to distoposterior part of cell; M_1 absent; CuA_1 and CuA_2 branched distad of cubitus beyond cell, extending in a slight curve to margin; CuP slightly evident basally; undersurface pale brown except for pale yellowish-brown costa; hindwing pale gray, with two acanthae in female; venation (Fig. 2) with Rs and M_1 stalked about ⅓ length beyond end of cell; M_2 closer to M_3 than to M_1; M_3 branched with CuA_1 beyond cell, about ¼ distance as Rs and M_1; CuA_2 arising from cell about ⅔ length of cubitus; 1A and 2A separate basally, forming an elliptical support.

Abdomen (Fig. 3): Male with squamiform sex scales on intersegmental membrane between abdominal terga 2–3.

Male genitalia (Figs. 4–5): Uncus narrow and elongate with few subapical setae; gnathos enlarged distally and forming a bulbous projection with subapical setae on lateral surface; genital capsule slightly tapered from base; valva with apicoventral area beyond sacculus membranous and setose, apex widely bifurcate, base of costa with digitate projection with several apical setae; sacculus curved apically; vinculum narrow, bifurcating at base to nearly 3 times width at ½ length; juxta fused ventrally with vinculum, widening distolaterally forming a ventral support for aedeagus; aedeagus widest near middle, slightly tapering toward apex; ductus ejaculatoris with several spirales; vesica with many microspinules and a large cornutus.

Female genitalia (Fig. 6): Papillae anales conical, with short and long setae intermixed; apophyses anteriores bifurcating into two thin posterior arms, one fusing with eighth tergum, and one fusing with eighth sternum; eighth sternum spinulate and setose; antrum funnel-shaped, spinulate, and with posterior margin entire, anterior ⅔ with longitudinal ridges above two internal flanges; inception of spiralled ductus seminalis near middle of corpus bursae; larger spirales at base, each gradually narrowing toward apical end; ductus seminalis with a spiralled internal support; internal support enlarged basally; accessory lobe opposite base of ductus seminalis, juxtaposed to large, elongate plate; corpus bursae sparsely spinulate, larger spinules near base of ductus seminalis.

Holotype.—♂, "Quepos, 30 m P[arque] N[acional] Manuel Antonio, Prov[incia] Punt[arenas], COSTA RICA, G. Varela & R. Zuniga, Oct 1990, L-S-370500, 449000"; "COSTA RICA, INBio, CRI000, 274960" [bar code label]; "INBio Genitalia Slide, Sex ♂, No. 490" [yellow label]. The holotype is deposited in the entomology museum at Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Heredia, Costa Rica.

Paratypes.—119 ♂, 2 ♀. All bar code data are "Costa Rica, INBio, CRI000, CRI001, or CRI002" ending with a 6-digit number; only the last digit of the prefix is given with the last 6-digit number. 6 ♂, "Quepos, 80 m, P[arque] N[acional] Manuel Antonio, Prov[incia] Punt[arenas], COSTA RICA, R. Zuniga, Ene 1991, L-S-370900, 448800"; "0564348"; "0564336"; "0366906"; "0564463"; "0564637"; "0366794"; "INBio Genitalia Slide, Sex ♂, No. 465"; 7 ♂, same except, "Feb 1991"; "0625779"; "0347231"; "0347206"; "0346903"; "0625780"; "0347168"; "0346923"; 1 ♂, 1 ♀, same except, "Mar 1993, G. Varela"; "1409702"; "1409698"; "INBio Genitalia

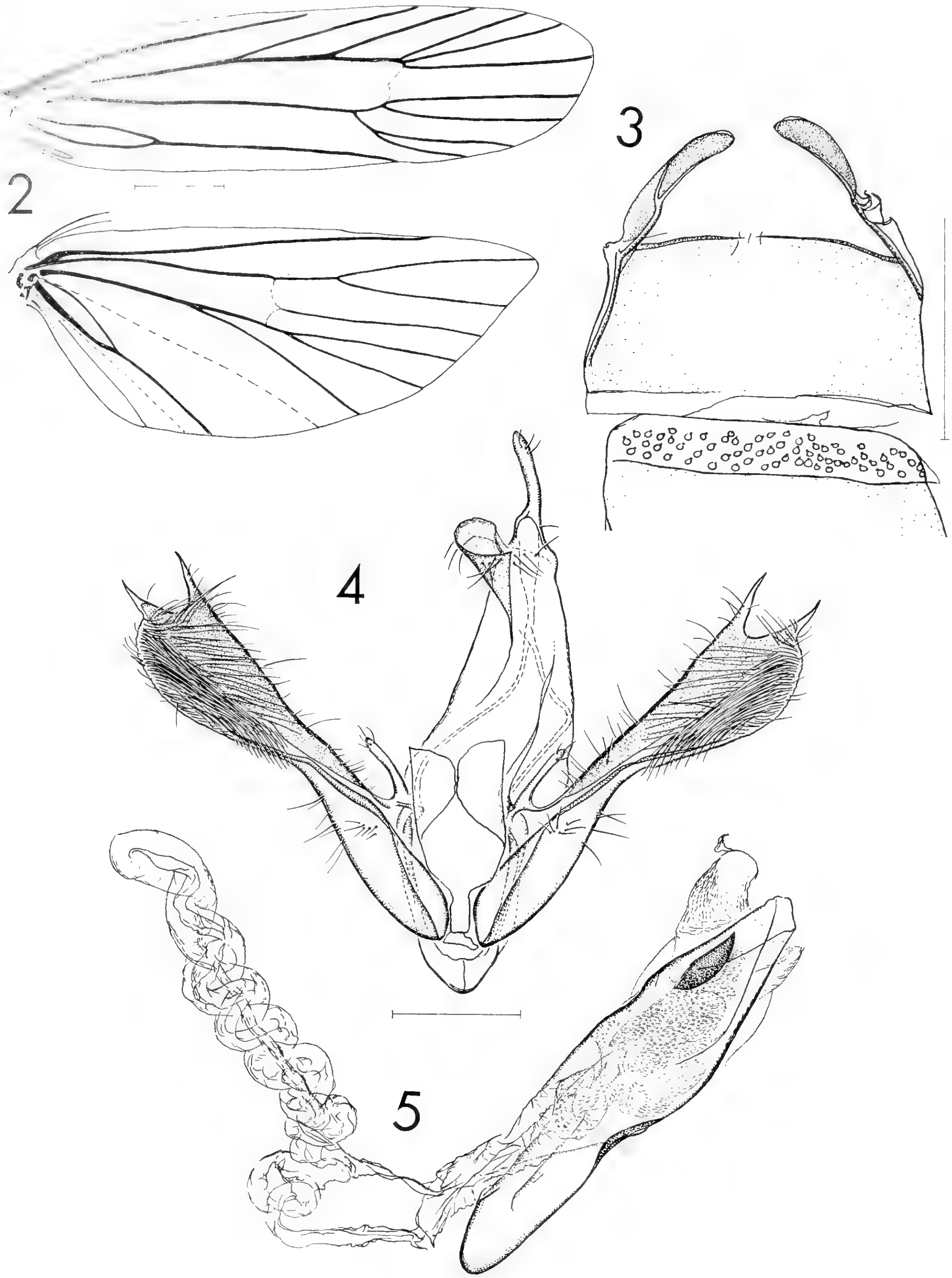

Fig. 2–5. *Glyphidocera guarou.* 2, Wing venation, female; scale line = 1.0 mm. 3, Male abdominal sex scales; scale line = 1.0 mm. 4–5, Male genitalia; scale line = 0.5 mm.

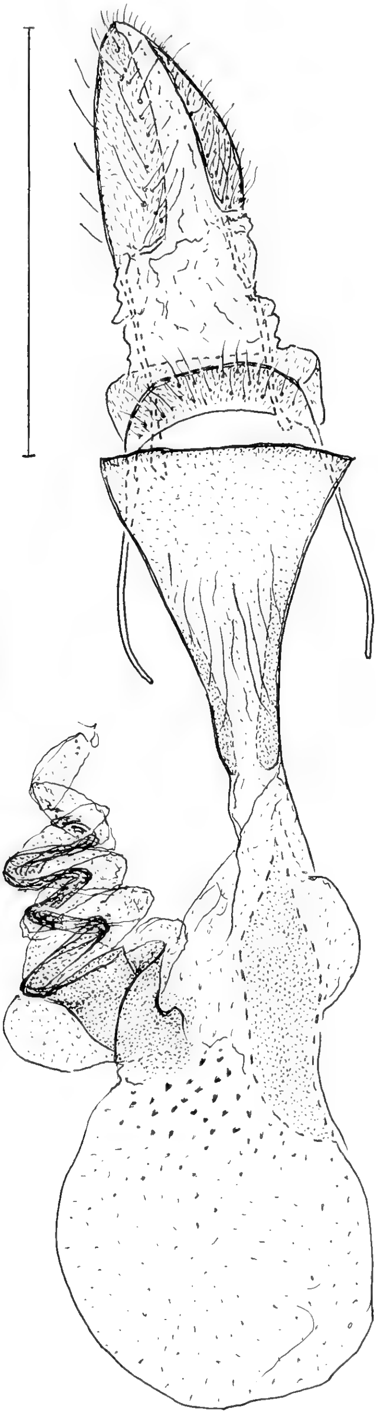

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Fig. 6. Female genitalia of *Glyphidocera guaroa*. Scale line = 1.0 mm.

Slide, Sex ♀, No. 427”; 1 ♂, same except, “R. Zuniga, Mar 1991”; “0648407”; 1 ♂, same except, “May 1991”; “1319436”; 1 ♂, same except, “Jul 1992, G. Varela”; “0950374”; “INBio Genitalia Slide, Sex, ♀, No. 426”; 1 ♂, same except, “R. Zuniga, Feb 1991”; “0347090”; 5 ♂, same except, “Ago 1993, G. Varela”; “1656013”; “1656023”; “1656008”; “1656012”; “1656082”; 1 ♂, same except, “1992”; “0940614”; 1 ♂, same except, “May 1991, R. Zuniga”; “1319472”; 1 ♂, “Se[p]t 1992, G. Varela”; “0815605”; 1 ♂, same except, “1993”; “1998326”; 1 ♂, same except, “1992, G. Zuniga”; “0935656”; 1 ♂, same except, “G. Varela & R. Zuniga, 1990”; “0223069”; 1 ♂, same except, “Nov 1990”; “0227948”; 6 ♂, same except, “Dic”; “0228703”; “0229104”; “0229072”; “0229266”, “0228770”; “0583981”; “INBio Genitalia Slide, Sex, ♂, No. 466”; 8 ♂, “Est[acion] Magsasay, P[arque] N[acional] Braulio Carrillo, 200 m, Prov[incia] Here[dia], COSTA RICA, R. Aguilar, Nov 1990, L-N-264600, 531100”; “0226705”; “0226773”; “0226735”; “0226738”; “0226721”; “0226729”; “0226693”; “0453154”; 2 ♂, same except, “R. Aguilar, Abr 1991”; “0275099”; “0275070”; 2 ♂, same except, “M. Zumbado, Oct 1990”; “0180818”; “0180807”; 2 ♂, same except, “A. Fernandez”; “0179675”; “0179638;” 1 ♂, same except, “R. Aguilar, Dic 1990”; “0701559”; 1 ♂, same except, “May 1991, M. A. Zumbado”, “1300398”; 1 ♂, “Est[acion] Pitilla, 700 m 9 km S Sta[tion] Cecilia, Prov[incia] Guan[acaste], COSTA RICA, P. Rios & C. Moraga, Oct 1990, L-N-330200, 380200”; “0197960”; 1 ♂, same except, “C. Moraga, Jul 1991”; “0300184”; 1 ♂, same except, “Ene 1995, #4354”; “2131715”; 1 ♂, same except, “P[arque] N[acional] Guanacaste, 700 m, 19–23 Jun 1993, P. Rios”; “1835123”; “INBio Genitalia Slide by D. Adamski, Sex, ♂, No. 479”; 4 ♂, “Est[acion] Sirena, 0–100 m, P[arque] N[acional] Corcovado, Prov[incia] Punt-

[arenas]. COSTA RICA, G. Fonseca, Se[p]t 1991, L-S-270500, 508300"; "0357571"; "0357617": "0357448"; "0357507"; 2 ♂, same except, "1990"; "0179079"; "0179187": 1 ♂, same except, "1991"; "0643420"; 2 ♂, same except, "Nov 1990"; "0183423"; "0183251"; 1 ♂, same except, "1993, #2490": "1625857"; 2 ♂, same except, "G. Fonseca, Dic 1992"; "0783807"; "0783813"; 1 ♂, same except, "1990"; "0297295"; 1 ♂, same except, "J.C. Saborio, 1991"; "0526635"; 1 ♂, same except, "G. Fonseca, Feb 1992"; "0621647"; 3 ♂, same except, "Mar 1992"; "0780383"; "0788594"; "0780480"; 2 ♂, same except, "Abr 1991"; "0475866"; "0475887"; 3 ♂, "same except, May 1991"; "0587949"; "0588114"; "0587822"; 1 ♂, same except, "1992"; "0914822"; 2 ♂, same except, "Jun 1991", "0646450"; "0646447"; 1 ♂, same except, "1992"; "0708208"; 4 ♂, "Sector Cerro Cocori, F[in]ca de E. Rojas, 150 m, Prov[incia] Limon, Costa Rica, E. Rojas, 31 Ene–21 Feb 1992, L-N-286000, 567500"; "0785313"; "0775096"; "0775089"; "INBio Genitalia Slide by D. Adamski, Sex, ♂, No. 471" [yellow label]; "0785137"; "INBio Genitalia Slide by D. Adamski, Sex, ♂, No. 470"; 1 ♂, same except, "1993"; "0402859"; 2 ♂, same except, "Feb 1993"; "0998918"; "0998790"; "INBio Genitalia Slide by D. Adamski, Sex ♂, No. 425"; 5 ♂, same except, "Mar 1992"; "0363635"; "0363719"; "0363734"; "0363593"; "0363629"; 1 ♂, same except, "1991"; "0181437"; 6 ♂, same except, "Abr 1992"; "0785544"; "0785511"; "0785518"; "0786302"; "0785501"; "INBio Genitalia Slide by D. Adamski, Sex ♂, No. 482"; "0786366"; "INBio Wing Slide by D. Adamski, Sex ♂, No. 429"; 1 ♂, same except, "May 1992"; "0373560"; 2 ♂, same except, "26 Jun a 16 Jul 1992"; "0703169"; "0745136"; 1 ♂, same except, "1993"; "1699131"; "INBio Genitalia Slide by D. Adamski, Sex ♂, No. 472"; 1 ♂, same except, "Se[p]t 1991"; "0598938"; 1 ♂, same except, "Se[p]t 1993"; "1141370"; 1 ♂, same except, "Oct 1992"; "0819686"; 6 ♂, same except, "Nov 1991"; "0501470"; "0501449"; "0460128"; "0460151"; "0460169"; "0460144"; 2 ♂, same except, "9 a 30 Nov 1992"; "0931418"; "0931463"; "INBio Wing Slide by D. Adamski, Sex ♂, No. 491"; 2 ♂, same except, "Dic 1991"; "0361269"; "0361205"; 1 ♂, same except, "30 Km N de Cariari, A.C. Tortuguero, Ene 1994"; "1856571." One hundred and five paratypes deposited in INBio and 15 paratypes deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Distribution.—*Glyphidocera guaroa* is widespread in Costa Rica, ranging from the coastal Pacific to the coastal Caribbean, and from the western province of Guanacaste east to the southeastern province of Puntarenas near Panama. It is likely that this species occurs elsewhere in Central America.

Etymology.—*Glyphidocera guaroa* is named for a Costa Rican liquor, güaro, that is made from sugar cane.

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THE *NEOPERLA CLYMENE* (NEWMAN) COMPLEX (PLECOPTERA: PERLIDAE) IN ILLINOIS, NEW STATE RECORDS, DISTRIBUTIONS, AND AN IDENTIFICATION KEY

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Abstract.—Stoneflies of the *Neoperla clymene* (Newman) species complex in Illinois were reexamined from museum and newly collected adult material. Seven species have historically been present in the state. The previously known species, *N. clymene,* is joined by six new state records including *N. catharae* Stark and Baumann, *N. harpi* Ernst and Stewart, *N. mainensis* Banks, *N. occipitalis* (Pictet), *N. robisoni* Poulton and Stewart, and *N. stewarti* Stark and Baumann. Four species (*N. mainensis, N. occipitalis, N. robisoni, and N. stewarti*) are considered extirpated since all records predate 1930. Two species (*N. catharae* and *N. clymene*) have had extensive range reductions, while *N. harpi* has maintained its historical distribution in the state. Large rivers at the periphery of Illinois and small streams in the Shawnee Hills of southern Illinois still maintain populations of *Neoperla.*

Key Words: Plecoptera, *Neoperla,* Illinois, identification key, extirpation

Neoperla in the Nearctic Region were viewed until recently as a single, wide-ranging and variable species, *Neoperla clymene* (Newman) (Stark 1990). Stark and Baumann (1978), Stark and Lentz (1988), and Ernst et al. (1986) split this complex into two species groups, *clymene* and *choctaw,* based on adult genitalic and egg structures, with 12 recognized species. Subsequent researchers (Ernst et al. 1986, Stark 1995, Smith and Stark 1998) have described three new species to bring the current North American total to 15.

Neoperla reside in relatively clean streams throughout the eastern half of North America (Stewart and Stark 1988). Vaught and Stewart (1974) found that *N. clymene* exhibited a univoltine-slow (no egg diapause) life cycle, while Ernst and Stewart (1985) recorded a late emergence for *Neoperla* spp. compared to other cohabitating perlids and a preference for trees as adult habitat. These life history attributes leave them susceptible to changes in local stream health including increases in summer water temperature, reduction in dissolved oxygen, increased imbeddedness of mineral substrates, and removal of natural riparian vegetation.

The Illinois Natural History Survey (INHS) established natural history collections late in the nineteenth century as a repository to document the fauna and flora of Illinois, the Midwest, and across the continent. The age of these collections makes them irreplaceable as documentation of the natural communities found before major degradation of the native landform took place. This is fortunate since extinctions, local and regional extirpations, and shrink-

Table 1. Spatial accuracy codes used for *Neoperla* localities in Illinois (Figs. 1–4).

Spatial Accuracy Code	Location Description from Labels
1	Known exact location
2	Small municipality (<50,000 population) or park, point usually placed at center of town or at waterfront if stream name included on label.
3	Land survey data (principal meridian, township, range, section) or large municipality (>50,000), taken as center of municipality or section.
4	County, plotted as center of county.

age of historical range are common responses of stonefly species across the continent.

Frison (1935) investigated the Illinois stonefly fauna for over two decades early in the twentieth century. Many sites were repeatedly visited and their stonefly assemblage was well documented. Among these collections are sufficient numbers of *Neoperla,* then identified exclusively as *N. clymene,* to accurately document the original species assemblage of this environmentally sensitive genus. Reevaluation of this material has recently been completed and the results presented herein. The objective of this study is to document the species of *Neoperla* present in Illinois. We hope, through providing a fully illustrated key to adults and eggs of regional species, that others locate additional populations of this environmentally sensitive genus. This study is part of a larger effort to update Frison's (1935) *The Stoneflies, or Plecoptera, of Illinois* over 60 years after its publication.

METHODS

Illinois *Neoperla* in the INHS insect collection were reevaluated using current literature. The task of tracking information about each specimen was simplified by a recently completed Plecoptera database that links species names, label data, and location information with a catalogue number. This database is now available in simplified form on the Internet (URL: www.inhs.uiuc.edu/cbd/EPT/index.html).

Poulton and Stewart (1991) reared and associated nymphs of six of seven Interior Highlands species. However, there are still eight species whose nymphs are either undescribed or inadequately known. Until further associations have been completed, the adults are necessary to definitively identify species in the complex. The tergal process, paraproct, and internal aedeagus are useful for identification of males. Relative length and degree of sclerotization of the spermathecum and the ornamentation of the egg chorion are important female characteristics.

Adult internal structures were viewed by clipping the abdomen from the body at about the fourth segment, then placing it in boiling 10% KOH until clear. Eggs were extracted before boiling and viewed using a compound microscope. In addition to the historical material, new specimens were obtained by rearing of nymphs, ultra-violet light trapping, and by sweeping streamside vegetation from many locations across the state.

Latitude and longitude coordinates for each unique location were recorded from a digital DeLorme® Street Atlas USA. Many records had vague localities, the exact locations of which were impossible to determine. So as not to lose any location data, locations were coded one through four for accuracy (Table 1). This accuracy was denoted on range maps as different sized symbols, usually with closed points and open circles of increasing size. Collection locations were stored in electronic format using FileMakerPro® software. Mapping of these locations was produced using ArcView® software.

ditionally, location information has been provided in the text of works such as these. We have opted to rely on the Plecoptera database web site for dissemination of this detailed and highly repetitive information. Those who do not have access to the Internet may request the information from the senior author in other formats.

RESULTS

Adult *Neoperla* accounted for 92 of the current 4,880 Illinois and 18,885 total Plecoptera records at the INHS (Table 2). A total of 411 adult specimens was reevaluated that represented 32 unique historical and contemporary locations (Fig. 1). Seven of the 15 species in the genus are now known to occur in Illinois (Table 2). Six belong to the *clymene* species group, while one belongs to the *choctaw* group. Six of these species are new state records and some represent sizable range extensions. The greatest concentration of both species and specimens were from the state's southern tip where stream gradients were high and overall stream health best. Despite the large range in latitude, 37.00° to 42.16°N, the majority of records indicated a mid-June through late July emergence for all species encountered. Illinois distributions, brief notes on general ecological requirements, and additional information on taxonomic characters are provided for each species.

Neoperla catharae Stark and Baumann
(Figs. 3, 5, 12)

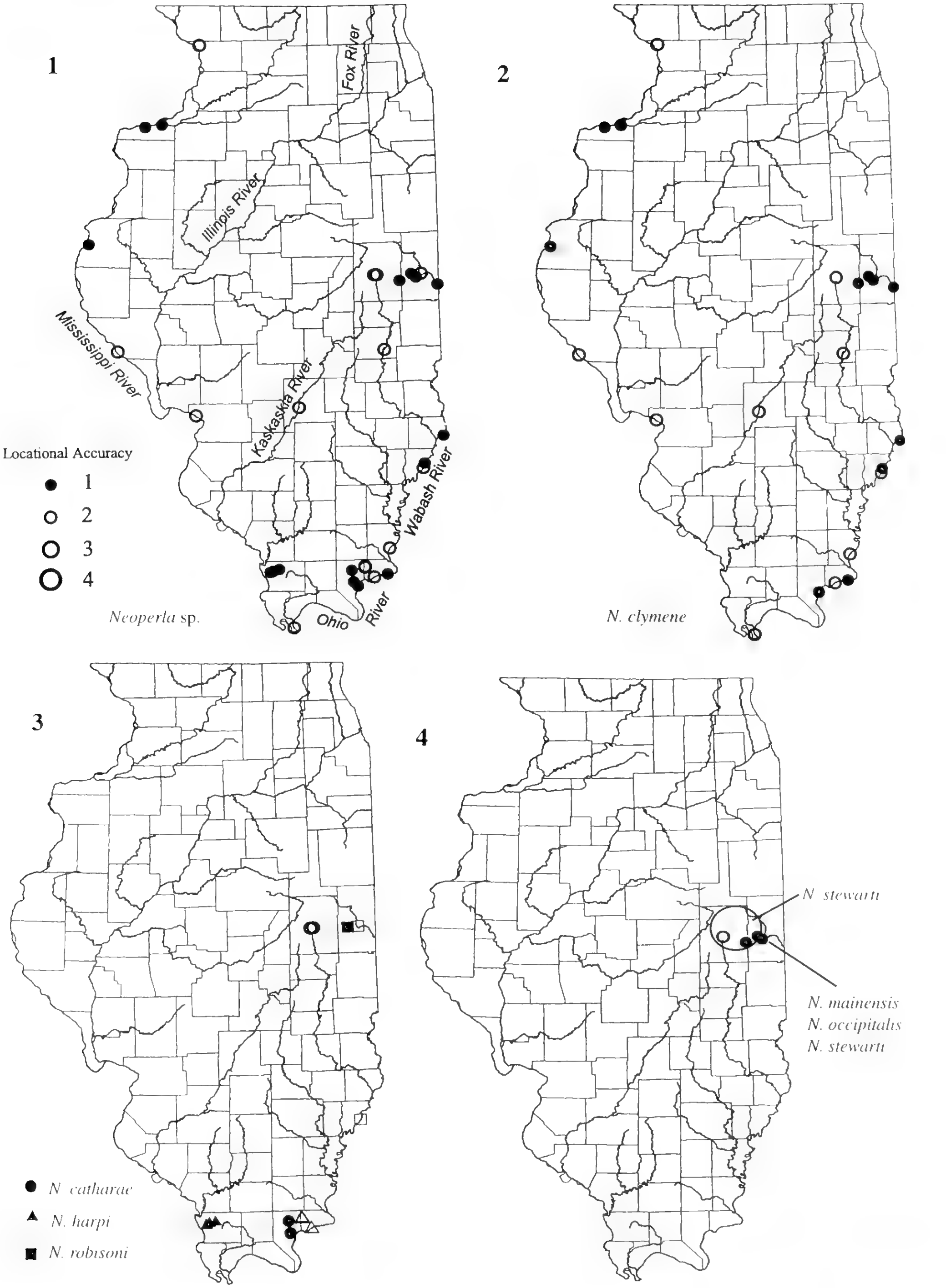
This species provided 7.6% of Illinois *Neoperla* records and 2.7% of all specimens (Table 2). This is the only member of the *N. choctaw* Stark and Baumann species group to be taken in Illinois. Its presence is a new state record. Historically, specimens were taken as far north as Champaign County, in the headwaters of the Embarras and Vermilion rivers (Fig. 3). The exact collection location has been coded with an accuracy code of two, which straddled streams in both drainages. All populations in the central Illinois Grand Prairie natural division (Schwegman 1973) appear to have been extirpated since no specimens have been taken since 1889.

Extant populations survive only in high quality streams in the Lusk Creek drainage of southern Illinois. The Shawnee National Forest buffers this area from agriculture and other development; therefore, the species is afforded some measure of protection against water quality degradation. Other populations may eventually be found further west in similar uplands of the Ozark Hills natural division along the Mississippi River. Its current range includes Alabama, Arkansas, Kentucky, Missouri, Ohio, Oklahoma, Pennsylvania, Tennessee, and Virginia (www.mc.edu/~stark/stonefly.html). No detailed life history information is available for this species (Stewart and Stark 1988). Ernst and Stewart (1985) found that it emerged later than its congeners, August through September, with males and females having negatively skewed and extended emergence patterns, respectively.

Neoperla clymene (Newman)
(Figs. 2, 6, 13)

Harris and Webb (1995) listed this species from Illinois. *Neoperla clymene* provided 35.9% of the records and 14.4% of the specimens and was the most widely distributed *Neoperla* in Illinois (Table 2, Fig. 2). It was most abundant in larger rivers such as the Wabash, Ohio, and Mississippi rivers, where it was recently common in light trap samples from a reach south of Rock Island. Several specimens were recently taken from the Vermilion River near the Indiana border. These represent the only contemporary specimens from small-to-medium sized rivers throughout middle Illinois (DeWalt et al. 1999).

Historically, the species was abundant in the Embarras, Kaskaskia, and Vermilion rivers (Fig. 3) of the Grand Prairie and Southern Till Plain of central Illinois. Stark (1990) reported it from throughout the



Figs. 1–4. *Neoperla* locations in Illinois. 1, All *Neoperla* locations in Illinois. 2, *N. clymene*. 3, *N. catharae*, *N. harpi*, *N. robisoni*, 4, *N. mainensis*, *N. occipitalis*, *N. stewarti*.

Table 2. *Neoperla* species found, number of adult records in Plecoptera database, number of individuals in INHS insect collection, and the number of unique sites across Illinois from which *Neoperla* species were taken.

Species	Records	Individuals	Unique Sites
Neoperla catharae Stark and Baumann 1978	7	11	4
Neoperla clymene (Newman) 1839	33	59	20
Neoperla harpi Ernst and Stewart 1986	18	235	7
Neoperla mainensis Banks 1948	2	2	1
Neoperla occipitalis (Pictet) 1841	1	1	1
Neoperla robisoni Poulton and Stewart 1986	3	18	3
Neoperla stewarti Stark and Baumann 1978	28	85	4
Total	92	411	32

southeastern United States and indicated that some older eastern and midwestern literature records should be viewed with doubt until specimens have been reexamined. He implied that they might have been confused with a newly named species, *N. osage* Stark and Lentz. Vaught and Stewart (1974) recorded an univoltine-slow life cycle for *N. clymene* in the Brazos River of west central Texas. Ernst and Stewart (1985) reported emergence characteristics for this species, but Stark and Lentz (1988) showed their studied population to be an undescribed species, *N. falayah* Stark and Lentz.

Neoperla harpi Ernst and Stewart
(Figs. 3, 7, 14)

This species is restricted to the southernmost tip of Illinois, in the Shawnee and Ozark Hills natural divisions (Fig. 3). Its presence represents a new state record. Despite representing only 19.6% of the records, it provided a disproportionate share, 57.2%, of the specimens examined. A robust population exists in the Hutchins Creek drainage near Wolf Lake, Illinois. Part of this drainage is protected within the La Rue–Pine Hills Ecological Area, a National Natural Landmark. Historical records also indicate its presence in the Shawnee Hills, farther to the east.

Poulton and Stewart (1991) considered this species an Ozark endemic. Ross (1944) spoke of the Ozark and Shawnee Hills natural divisions as extensions of the Missouri Ozarks, and therefore, it is not surprising to find this species in southern Illinois. Stark (1990) listed Arkansas, Missouri, and Oklahoma as locations for this species. Poulton and Stewart (1991) collected adults from late May through late August, but no additional life history data are available.

Neoperla mainensis Banks
(Figs. 4, 8, 15)

The species is represented by two records consisting of two females (Table 2) from Frison's (1935) famous Oakwood, Illinois location on the Salt Fork of the Vermilion River (Fig. 4). *Neoperla mainensis* is the only known member of the *clymene* group that has a notched, triangular subgenital plate, thus, we feel confident in our determination. Its presence in Illinois represents a new state record and a significant range extension from the known localities of Ohio, Maine, and Ontario (Stark 1990). No specimens have been collected since 1927; therefore, we feel that it has been extirpated from Illinois. No life history data are available for this species (Stewart and Stark 1988).

Neoperla occipitalis (Pictet)
(Figs. 4, 9, 16)

This species was taken as a single female (Table 2) from the Oakwood location (Fig. 4). Its presence represents a new state record. It has not been collected since 1925; therefore, it appears to have been extirpated from Illinois. It is known from much of the

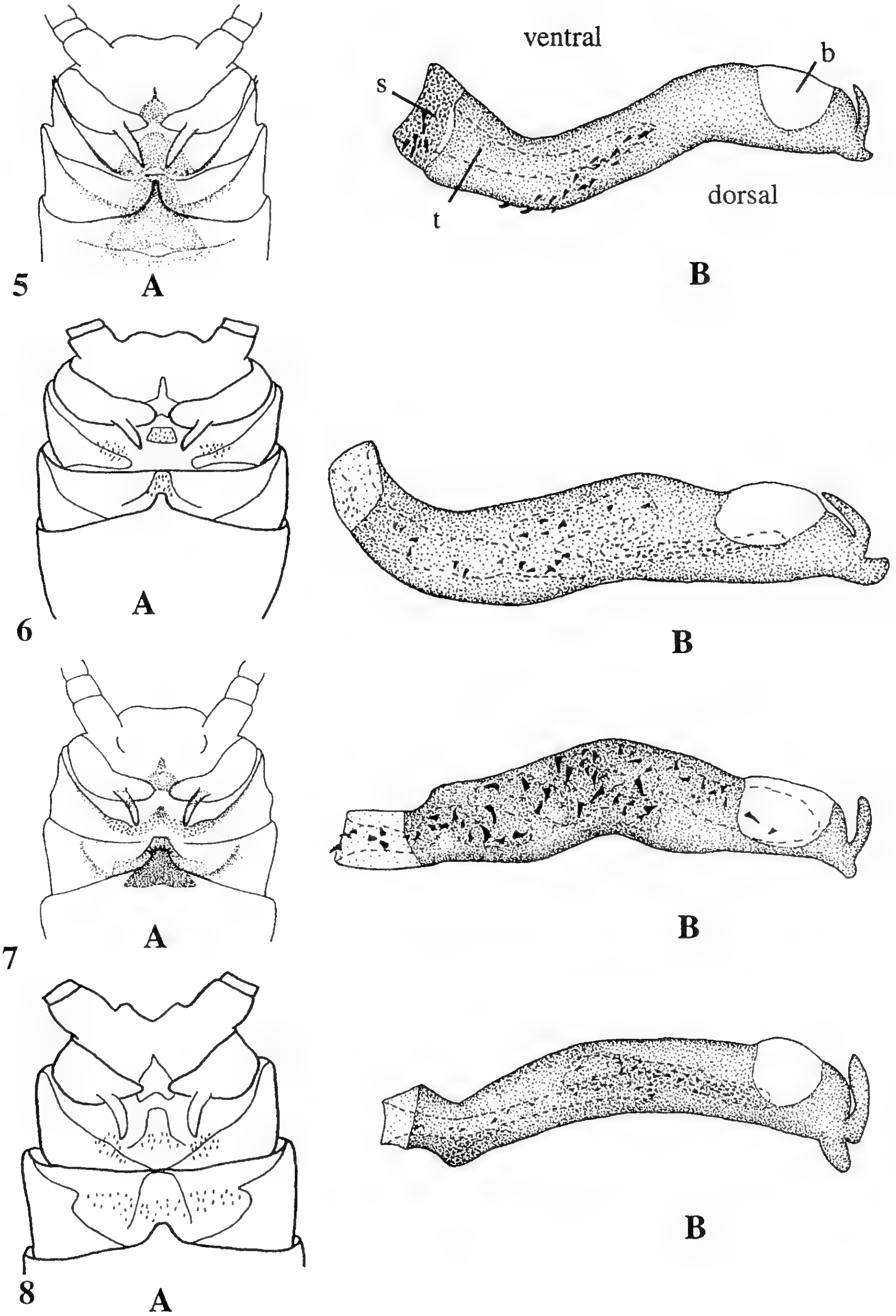


Fig. 5–8. Male structures of *Neoperla* spp. A = abdominal terga 7–10; B = aedeagus, lateral. 5, *N. catharae*. 6, *N. clymene*. 7, *N. harpi*. 8, *N. mainensis*. Abbreviations: b = bulb, t = tube, s = sac. Figures 5A and 7A modified from Poulton and Stewart (1991); Figures 6A and 8A modified from Stark and Baumann (1978).

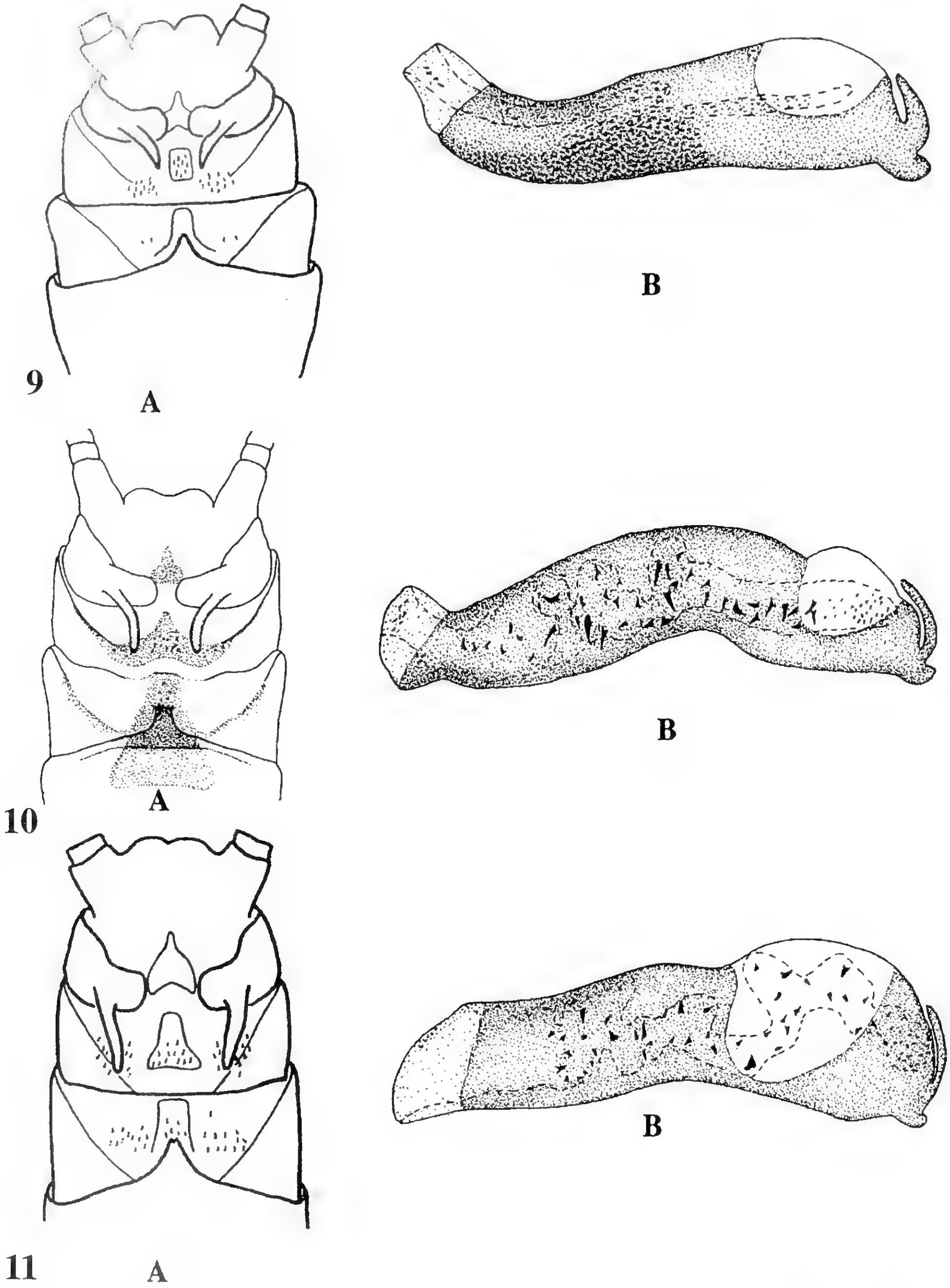


Fig. 9–11. Male structures of *Neoperla* spp. A = abdominal terga 7–10; B = aedeagus, lateral. 9, *N. occipitalis.* 10, *N. robisoni.* 11, *N. stewarti.* Figure 10A modified from Poulton and Stewart (1991); Figures 9A and 11A modified from Stark and Baumann (1978).

Great Lakes region, where it is apparently common, and from as far south as northern Alabama and Mississippi (Stewart and Stark 1988). No life history information is available for this species (Stewart and Stark 1988).

Neoperla robisoni Poulton and Stewart (Figs. 3, 10, 17)

This species represented 3.3% of records and 4.4% of Illinois *Neoperla* specimens (Table 2). Its presence constitutes a new state record, but since it has not been collected since 1939, it is probably extirpated from the state. Historically, this species resided in the Vermilion and Wabash river basins of east central Illinois (Fig. 3). Its published distribution includes Arkansas, Mississippi, Missouri, Oklahoma, and Tennessee (Stark 1990). Stewart et al. (1974) listed *N. clymene* from New Mexico, which was subsequently identified by Stark (1990) as *N. robisoni*. Stark (1990) has raised doubt as to the validity of the label data associated with any *Neoperla* specimens found in New Mexico. Poulton and Stewart (1991) and Ernst et al. (1986) found that *N. robisoni* primarily inhabited Gulf Coastal Plains streams, emerging in late May and through June. No detailed life history data are available for this species (Stewart and Stark 1988).

Neoperla stewarti Stark and Baumann (Figs. 4, 11, 18)

This species represented 30.4% of records and 20.7% of the individuals (Table 2). It is also a new state record. It has not been collected in Illinois since 1930, and is feared extirpated from the state. Historically, it was locally abundant in the Vermilion River drainage of eastern Illinois (Fig. 4). Previous records are for Alabama, Kentucky, Maine, Minnesota, Mississippi, Ohio, Pennsylvania, Tennessee, Virginia, and Wisconsin (Stark 1990).

Difficulty in identification may arise with some females due to the presence of a parasitoid wasp, the pupa of which usually develops in the spermathecum. Distortion of this organ gives the mistaken appearance of a *choctaw* complex species by darkening and expanding the very tip of the spermathecum. Parasitism rates ranging from 10 to 50% were observed. The pupa was large enough to completely block the spermathecum and questions the efficacy of mating for afflicted specimens. No life history data are available for this species (Stewart and Stark 1988).

DISCUSSION

The number of stonefly species known from Illinois has changed considerably since Harris and Webb (1995) published an updated nomenclature and listed 63 species for the state. DeWalt and Stark described *Perlesta golconda* (in DeWalt et al. 1998) and DeWalt et al. (2001) added six state record *Perlesta* species for a new total of 70. The addition of the new *Neoperla* species brings the total to 76 species.

The perlid stonefly genus *Perlesta* was found to contain at least eight species in Illinois (DeWalt et al. 2001). These species appear to be relatively unaffected by the large-scale anthropogenic disturbance of the Illinois landscape. In fact, one species has moved into Illinois over the past three decades. A rather different scenario has unfolded for *Neoperla* species. It appears that four of the seven species now known from the state, have been extirpated (*N. mainensis, N. occipitalis, N. robisoni, and N. stewarti*). Additionally, two have experienced apparent range reductions (*N. clymene* and *N. catharae*), while only one (*N. harpi*) appears to have maintained its historical range.

This differential response to changes in the Illinois landscape is intriguing. *Neoperla* typically reside in relatively clean streams in Illinois and in the Interior Highlands (Poulton and Stewart 1991). Hilsenhoff (1987) and Lentz (1993) have provided pollution tolerance values that rank *Neoperla* as highly sensitive to environmental degradation. *Neoperla clymene* exhibits an

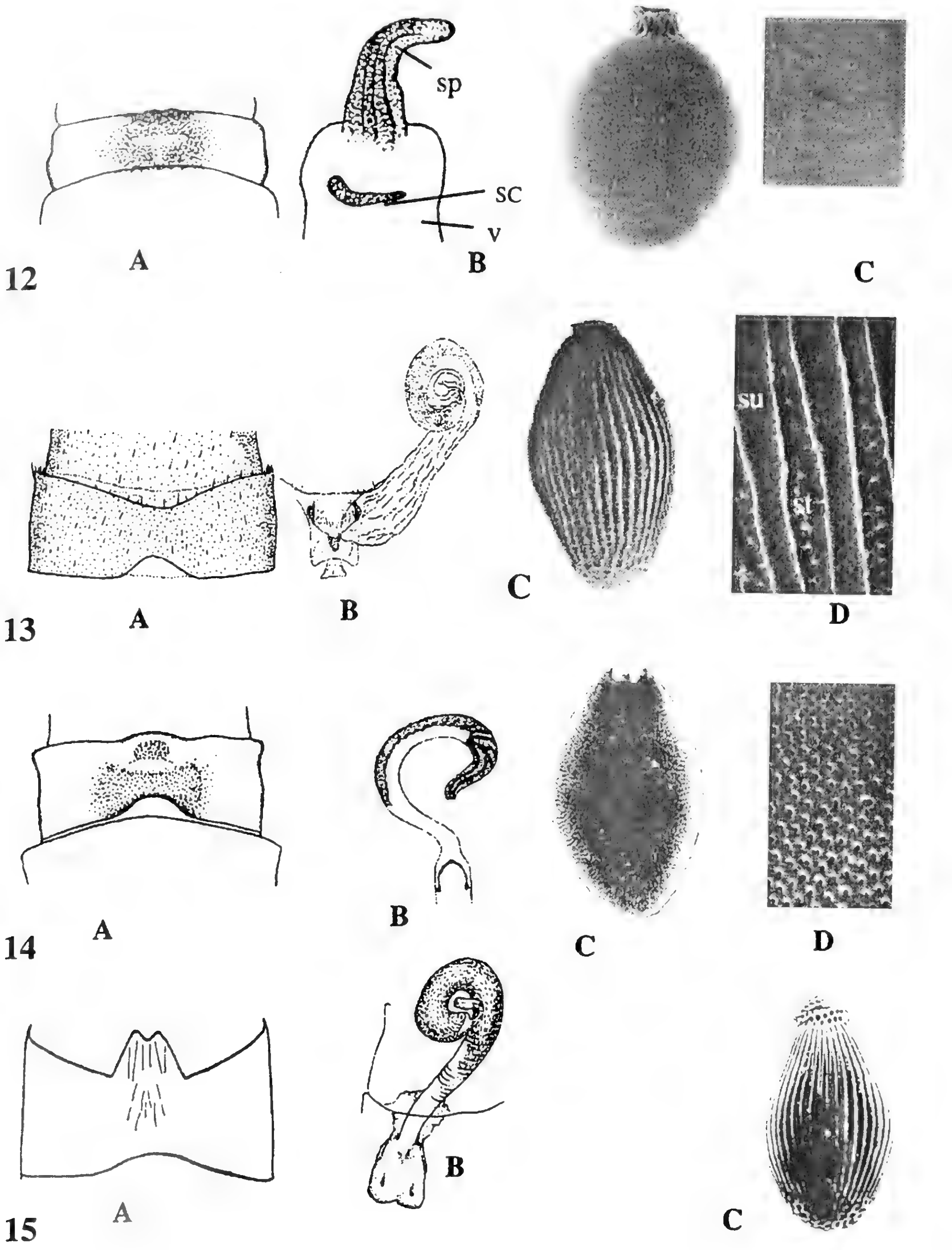


Fig. 12–15. Female and egg structures of *Neoperla* spp. A = abdominal sternite 8 and subgenital plate; B = spermathecum; C = egg; D = detail of egg chorion. 12, *N. catharae*. 13, *N. clymene*. 14, *N. harpi*. 15, *N. mainensis*. Abbreviations: sc = sclerite, sp = spermathecum, str = striae, su = sulci, v = vagina. Figures 12A, 12B, 14A, and 14B modified from Poulton and Stewart (1991); 13A-D from Stark (1990); 12C and 14C from Ernst et al. (1986); and 15A and 15C from Stark and Baumann (1978).

univoltine-slow life cycle, eggs hatch soon after being laid, and nymphs grow throughout the majority of the year (Vaught and Stewart 1974). In that study, no egg diapause was present, unlike what has been shown for *Perlesta decipiens* (Walsh) (Snellen and Stewart 1979). Diapause presumably permits this species to carry the generation through poor environmental conditions such as high summer water temperatures, low dissolved oxygen, or intermittent flow. The presumed lack of diapause in the rest of *Neoperla* species, and any other stonefly with a similar life history, would make them highly susceptible to changes in local land use including stream channelization and removal of riparian trees. This very scenario has taken place in streams across the rich fertile prairies of Illinois, where most of the species' loss and range reductions have taken place for *Neoperla.* It is doubtful that the extirpated species will again live in Illinois streams within the near future. The 'islands' of suitable habitat from which recolonization could occur, even if the conditions of streams in the state were to improve dramatically, are so distant that the species may not bridge the gap. The kind of stream habitat fragmentation that exists in Illinois, and elsewhere in the Midwest, puts the healthy islands at risk of high extinction rates and limits rates of emigration (Zwick 1992). Thankfully, some protection is afforded to those remaining populations of *Neoperla* in southern Illinois, since much of the land is in the Shawnee National Forest.

To facilitate identification of *Neoperla* in Illinois and neighboring states, a key to adults and eggs of the seven known species is provided. This key is modified from Poulton and Stewart (1991) and Stark and Lentz (1988).

KEY TO ADULTS AND EGGS OF ILLINOIS *NEOPERLA*

1. Male aedeagal tube with external spines (Fig. 5B); anterior margin of female sternum 8 entire (Fig. 12A); female spermathecum short, not coiled (Fig. 12B); egg chorion smooth (Fig. 12C) . . . . *N. catharae*
– Aedeagal tube without external spines (Fig. 6B); female sternum 8 with rectangular, triangular, or sub-circular indentation along anterior margin (Fig. 13A); female spermathecum long, atleast partially coiled (Fig. 13B); egg striate or punctate (Fig. 13C, 14C); *Neoperla clymene* group 2
2. Tergum 10 with anteriorly directed genital hooks (Fig. 6A), males 3
– Tergum 10 without genital hooks, females . . 8
3. Aedeagal tube abruptly bent ventrad near midlength (Fig. 7B) 4
– Aedeagal tube straight or slightly sinuate without abrupt bend at midlength (Fig. 6B) 5
4. Aedeagal tube apex abruptly constricted (Fig. 7B) . . . . *N. harpi*
– Aedeagal tube apex as wide as or wider than subapical area (Fig. 10B) . . . . *N. robisoni*
5. Aedeagal tube short and plump, length about 3× width at bulb (Fig. 11B) . . . . . *N. stewarti*
– Aedeagal tube slender, length about 4–6× width at bulb (Fig. 6B) 6
6. Aedeagal tube apex with prominent knob (Fig. 8B) . . . . *N. mainensis*
– Aedeagal tube apex without knob (Fig. 6B) 7
7. Dorsal midlength of tube with prominent patch of spicules, sac armed with very small spines (Fig. 9B) . . . . *N. occipitalis*
– Dorsal midlength of tube without prominent patch of spicules, sac with large spines (Fig. 6B) . . . . *N. clymene*
8. Posteromesal margin of sternum 8 recessed, not projecting beyond posterolateral margins (Fig. 13A) . . . . *N. clymene*
– Posteromesal margin of sternum 8 projecting beyond posterolateral margins (Fig. 14A) . . 9
9. Spermathecal stalk lining forming an irregular, jagged inner margin (Fig. 14B); egg nonstriate, but coarsely punctate (Fig. 14C) . . . . *N. harpi*
– Spermathecal stalk lining not forming jagged margin (Figs. 17B, 18B); egg striate (Figs. 15C–18C) 10
10. Subgenital plate triangular and apically notched (Fig. 15A) . . . . *N. mainensis*
– Subgenital plate a small truncate tab or otherwise slightly convex surface, not notched at apex (Figs. 16A–18A) 11
11. Setal lining of spermathecum restricted to a small apical patch (Fig. 18B) . . . . . *N. stewarti*
– Setal lining not restricted to apical patch, usually extends >⅓ length of spermathecum (Figs. 16B, 17B) 12

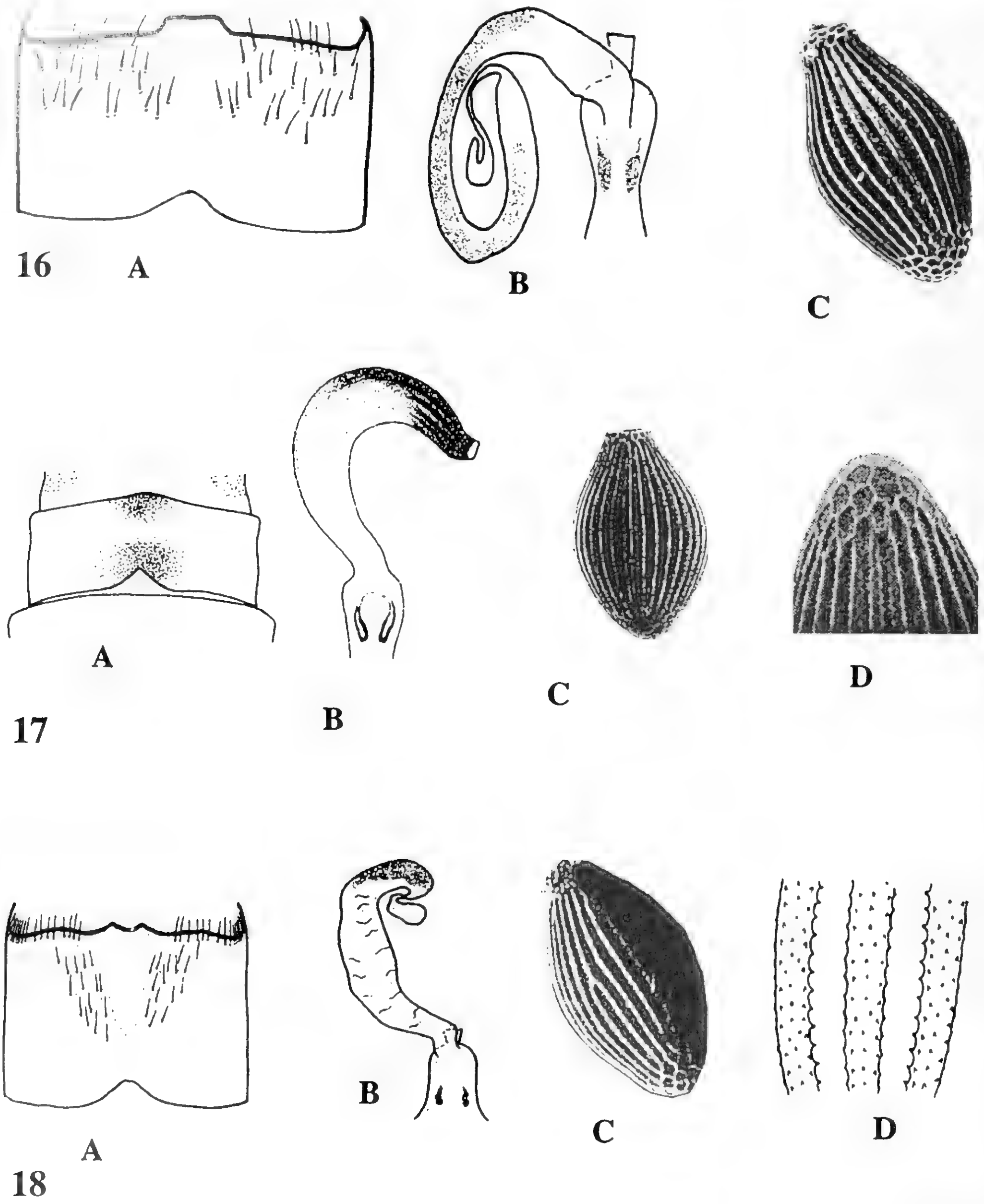


Fig. 16–18. Female and egg structures of *Neoperla* spp. A = abdominal sternite 8 and subgenital plate; B = spermathecum; C = egg; D = detail of egg chorion. 16, *N. occipitalis*. 17, *N. robisoni*. 18, *N. stewarti*. Figures 17A and 17B modified from Poulton and Stewart (1991); 17C and 17D from Ernst et al. (1986); and 16A–D and 18A–C from Stark and Baumann (1978).

12. Spermathecal stalk lining tapered to a rounded apex and without darkened longitudinal ridges (Fig. 16B) . . . . *N. occipitalis*
– Spermathecal stalk lining truncate apically and with 2–3 folds forming dark longitudinal ridges (Fig. 17B) . . . . *N. robisoni*

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NEW DISTRIBUTIONAL AND HOST-PLANT RECORDS FOR THE HETEROPTERANS *AUFEIUS IMPRESSICOLLIS* STÅL (RHOPALIDAE) AND *PRIONOSOMA PODOPIOIDES* UHLER (PENTATOMIDAE) IN THE SOUTHEASTERN UNITED STATES, WITH NOTES ON THEIR WESTERN UNITED STATES HOSTS

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Abstract.—The rhopalid *Aufeius impressicollis* Stål and pentatomid *Prionosoma podopioides* Uhler, native to western North America, were not known east of the Mississippi River until the early twentieth century and were first reported from the Southeast (South Carolina) in 1988. New state records for *A. impressicollis* are Georgia and North Carolina, and North Carolina is a new state record for *P. podopioides*; additional South Carolina records are given for both species. Most collections of *A. impressicollis* in the Southeast were from *Amaranthus palmeri* S.Wats.; host plants in California were other species of Amaranthaceae plus Chenopodiaceae. Southeastern collections of *P. podopioides* were from crowns of bunchgrasses growing near its main hosts, *Plantago aristata* Michx. and *P. wrightiana* Dcne. Adults in Oklahoma and Texas were taken on *P. patagonica* Jacq. and *P. rhodosperma* Dcne.; Oklahoma and Texas also are new state records.

Key Words: insect distribution, Rhopalidae, Pentatomidae, host-plant relationships

The rhopalid *Aufeius impressicollis* Stål and pentatomid *Prionosoma podopioides* Uhler are little-known, mainly western North American heteropterans. Eastern U.S. records for both species are scant. Ohio, the first eastern record for *A. impressicollis* (Osborn and Drake 1915), remained the easternmost record until it was reported from Maryland (Wheeler 1984). The first southeastern record was South Carolina (Wheeler 1988). Blatchley's (1926) manual of eastern U.S. Heteroptera did not include *P. podopioides*; at the time, its easternmost records—Iowa and Missouri (Stoner 1916, 1920)—were west of the area treated by Blatchley (east of 90th meridian). Previously published records of *P. podopioides* east of the Mississippi River now include Michigan (McPherson 1970), Illinois (McPherson and Cuda 1975), and South Carolina (Wheeler 1988).

Here I provide additional southeastern records of *A. impressicollis* and *P. podopioides* and, based on observations in eastern and western states, notes on their habitats and host plants. Adults of both species were collected at all sites; sites at which nymphs of *A. impressicollis* were observed with adults are indicated by asterisks. Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Aufeius impressicollis Stål 1870

New southeastern U.S. records.—GEORGIA: *Jefferson Co., Rt. 1, 2.8 km NE of Wrens (33°13.5′N, 82°22.0′W), 15 Oct. 2000; McDuffie Co., Rt. 78, 2.7 km W of Harlem (32°25.2′N, 82°20.5′W), 15 Oct. 2000; *Richmond Co., Rt. 1, 3.8 km NNE of Blythe (33°19.4′N, 82°11.1′W), 15 Oct. 2000.

NORTH CAROLINA: Montgomery Co., Rt. 220, 5 km S of Emery (35°12.1′N, 79°43.6′W), 16 May 1999. SOUTH CAROLINA: *Aiken Co., Rt. 25, 0.1 km S of Edgefield Co. line, 9 km N of North Augusta (33°35.2′N, 81°56.5′W), 15 Oct. 2000; Calhoun Co., Rt. 6, 16 km NW of St. Matthews (33°41.8′N, 80°56.4′W), 21 Oct. 2000; Darlington Co., Rt. 34, 4.7 km W of Darlington (34°18.0′N, 79°55.4′W), 4 Nov. 2000; Dillon Co., Rt. 917, 3.6 km W of Latta (34°20.3′N, 79°28.2′W), 4 Nov. 2000; Edgefield Co., CR 407 nr jct. CR 37, 8.5 km SW of Eureka (33°39.5′N, 81°51.6′W), 28 Nov. 1998; Rt. 25, 3.9 km SSW of Trenton (33°42.7′N, 81°51.3′W), 15 Oct. 2000; Greenville Co., SR 50, 0.3 km N of Rt. 418, 4.5 km NW of Fork Shoals (34°38.4′N, 82°21.1′W), 29 Oct. 2000; Kershaw Co., Rt. 34, 5.5 km E of Camden (34°14.3′N, 80°32.9′W), 4 Nov. 2000; Lee Co., jct. Rt. 34 & CR 39, 0.5 km W of Una (34°16.1′N, 80°08.2′W), 4 Nov. 2000; Rt. 15, 2 km SW of Bishopville (34°12.4′N, 80°15.9′W), 4 Nov. 2000; Lexington Co., Rt. 302, 2 km NNE of Pelion (33°46.8′N, 81°14.3′W), 21 Oct. 2000; Marion Co., Rt. 76, Marion (34°10.7′N, 79°22.6′W), 2 Nov. 2000; *Orangeburg Co., Rt. 178, 2.3 km NNE of North (33°37.0′N, 81°04.7′W), 21 Oct. 2000; Sumter Co., Rt. 261, 4.2 km S of Wedgefield (33°51.4′N, 80°30.9′W), 26 May 1999; Wedgefield (33°53.5′N, 80°31.1′W), 21 Oct. 2000.

Habitats and host plants.—Southeastern collections were from disturbed sites such as roadsides and cotton and soybean fields, mainly in the fall-line sandhills. The collection from Greenville Co., S.C., was in the piedmont.

An adult was beaten from the crown of weeping lovegrass (*Eragrostis curvula* [Schrad.] Nees; Poaceae) in North Carolina, and adults were on fruits of Mexican tea or wormseed (*Chenopodium ambrosioides* L.; Chenopodiaceae) southwest of Eureka, Edgefield Co., S.C. All other collections were from Palmer's amaranth (*Amaranthus palmeri* S. Wats.; Amaranthaceae), the host plant on which this rhopalid was found initially in the Southeast (Wheeler 1988).

In the western United States, an adult was beaten from the crown of weeping lovegrass in late April 2000 at each of three sites: Carter (34°11.2′N, 97°00.6′W) and Woodward (36°15.5′N, 99°09.7′W) counties in Oklahoma (new state record) and Gaines Co., Tex. (32°37.2′N, 102°38.4′W). In late May 2001, an adult was found in the crown of weeping lovegrass in Terry Co., Tex. (33°13.7′N, 102°09.1′W). In California in mid-August 1998, nymphs and adults were on tumble pigweed (*A. albus* L.) in Fresno County (36°51.7′N, 120°27.8′W), and on prostrate pigweed (*A. blitoides* S. Wats.) in San Benito County (36°56.8′N, 121°23.4′W). Host plants—that is, species on which nymphs were found—in a sparsely vegetated gravel lot at the Port of Stockton, San Joaquin County (37°57.1′N, 121°19.3′W), in mid-August 1998 were *A. albus, A. blitoides, C. ambrosioides,* and Russian thistle (*Salsola tragus* L.; Chenopodiaceae). Nymphs and adults appeared to be more numerous on and under the amaranths *A. albus* and *A. blitoides* than they were on the chenopods *C. ambrosioides* or *S. tragus.*

Prionosoma podopioides Uhler 1863

New southeastern U.S. records.—NORTH CAROLINA: Moore Co., Aberdeen (35°07.9′N, 79°26.0′W), 25 Aug. 1996; Richmond Co., Rt. 1, 2.4 km NNE of Marston (35°00.3′N, 79°34.0′W), 25 Aug. 1996, 12 July 1998. SOUTH CAROLINA: Chesterfield Co., Rt. 1, Middendorf (34°31.3′N, 80°09.5′W), 11 July & 6 Sept. 1998; Edgefield Co., CR 407 nr jct. CR 37, 8.5 km SW of Eureka (33°39.5′N, 81°51.6′W), 27 June & 28 Nov. 1998, 12 May 2001; Fairfield Co., Rt. 34, 0.6 km W of Kershaw Co. line, 12.6 km SSE of Ridgeway (34°16.4′N, 80°49.9′W), 20 May 2000.

Habitats and host plants.—All southeastern collections were from the fall-line sandhills. *Plantago aristata* Michx., a known host plant (Wheeler 1988), was present at all sites in North Carolina and South Carolina, but the pentatomid was collected from bunchgrasses within one or two m of bracted plantain, except in May 2001 when two third instars were found on a new host, Wright's plantain (*P. wrightiana* Dcne.), in Edgefield Co., S.C. In North Carolina, four adults were beaten from crowns of weeping lovegrass in Richmond County, and an adult was beaten from weeping lovegrass in Moore County. In South Carolina, crowns of weeping lovegrass yielded three adults in Chesterfield County and an adult (28 Nov.) in Edgefield County. An adult also was beaten from the crown of broomsedge (*Andropogon virginicus* L.; Poaceae) in Fairfield County. In Edgefield County, an adult also was swept from the inflorescences of southern jointweed (*Polygonella americana* [Fisch. & Mey.] Small; Polygonaceae).

In the western United States, I collected an adult of *P. podopioides* in Oklahoma (new state record) from the crown of *Andropogon* sp. in Dewey County (35°58.0′N, 98°58.6′W) on 26 April 2000 and three adults from woolly plantain (*Plantago patagonica* Jacq.) in Woodward County (36°19.2′N, 99°20.1′W) on 25 June 1999; in Texas (new state record) an adult was found on redseed plantain (*P. rhodosperma* Dcne.) in Scurry Co. (32°53.4′N, 101°03.9′W), on 25 May 2001. If nymphal development occurs on redseed plantain and woolly plantain, these plants are new host records for *Prionosoma podopioides.*

Discussion

Although they belong to different heteropteran families, *A. impressicollis* and *P. podopioides* are similar in having been described more than 130 years ago and in being seldom collected and poorly known throughout their current ranges. Both the rhopalid and the pentatomid also belong to monotypic genera, are considered western species that are recent additions to the fauna of the southeastern United States, develop frequently on western plants that are naturalized in the East, and are narrowly host specific.

Amaranthus palmeri, the only plant species on which nymphs of *Aufeius impressicollis* have been collected in the Southeast (Wheeler 1988), is indigenous to the Southwest or southern Great Plains (e.g., Muenscher 1980, Great Plains Flora Association 1986). Correll and Johnston (1970) remarked that *A. palmeri* is rarely adventive in the eastern United States, but since 1974, this plant has become an increasingly important weed in crops such as cotton, peanut, and soybean in the southeastern states (Webster and Coble 1997). Because nymphs of *A. impressicollis* were found on several chenopods in California, the host range of this rhopalid appears also to include the Chenopodiaceae, a family closely related to the Amaranthaceae (e.g., Heywood 1993, Takhtajan 1997).

I assumed that one of the rhopalid's chenopodiaceous hosts in California was *Salsola tragus* and did not submit the plant for identification. In California, however, Russian thistle consists of genetically divergent populations, one of which is unnamed. The more widespread species is true *S. tragus* (Ryan and Ayres 2000).

An important host of *P. podopioides* in the Southeast is bracted or buckhorn plantain (*Plantago aristata*; Plantaginaceae) (Wheeler 1988), a plant of disturbed habitats, particularly dry roadsides and sandy soils (e.g., Harper 1944, Johnson 1981). This plant might be native to the southwestern states or South America (Harper 1944). Gleason and Cronquist (1991) listed the original U.S. range of bracted plantain as Illinois to Louisiana and Texas, noting that it is naturalized farther east. *Plantago aristata* was not recorded from the southeastern states until the 1860s (Harper 1944, Fernald 1950).

Another western heteropteran that recently became established in the eastern United States, *Catorhintha mendica* Stål, apparently tracked the eastern spread of its principal host, wild four o'clock (*Mirabilis nyctaginea* [Michx.] MacMill.; Nyctaginaceae) (Balduf 1957, Hoebeke and Wheeler 1982). Whether the eastward spread of either *A. impressicollis* or *P. podopioides* was as host dependent as that of *C. mendica* is unknown.

Both the rhopalid and pentatomid also were beaten from the crowns of bunchgrasses, especially those of *Eragrostis curvula.* In the southeastern states, the well-developed crowns of this African grass provide shelter and overwintering sites for numerous native heteropteran species (Wheeler 1999; AGW, unpublished data).

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DESCRIPTIONS OF *TEPHRITIS FOOTEI* AND *T. HEADRICKI*, NEW SPECIES (DIPTERA: TEPHRITIDAE), WITH NOTES ON THEIR LIFE HISTORIES IN SOUTHERN CALIFORNIA

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Abstract.—***Tephritis* footei Goeden, n. sp.,** is a fruit fly (Diptera: Tephritidae) producing a single, annual generation in the flower heads of *Artemisia tridentata* Nuttall (Asteraceae) belonging to the subtribe Artemisiinae of the tribe Anthemideae in southern California. The egg, first-, second- and third-instar larvae and adults are described and figured, and selected characteristics of these stages are compared with those of other southern California *Tephritis.* Another new species of *Tephritis* belonging to the "*araneosa* complex", like *T. footei,* also is described: ***T. headricki* Goeden, n. sp.** Host plants of *T. headricki* belong to the genus *Solidago* of the subtribe Solidagininae of the tribe Astereae. The adults of these two new species are distinguished by a combination of characters involving oviscape lengths, wing patterns, wing lengths, and leg colors. The egg of *T. footei* is covered by a smooth, membraneous sheath of unknown function. The partial description of the first instar of *T. footei* is the second such for this instar in the genus *Tephritis.* Noteworthy for the first instar is confirmation of the fusion of the integumental petal with the stomal sense organ of *T. footei,* like that of *T. teerinki* Goeden. Similarly, the partial description of the second instar also is only the second for the genus *Tephritis.* The third instar has the fewest number of minute acanthae and the most integumental petals circumscribing the prothorax among four other described species. The lower, lateral, integumental petal of the cephalothorax continues around the oral cavity, like that of the third instar of *T. teerinki.* The life cycle is of the aggregative type and overwintering occurs as long-lived, sexually immature adults.

Key Words: Insecta, *Tephritis, Artemisia, Solidago,* Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of adults and immature stages, flower-head feeding, aggregative life cycle, seed predation, parastoids

To date, the life histories and immature stages of four species of *Tephritis* have been described in detail from southern California: *T. arizonaensis* Quisenberry (Goeden et al. 1993), *T. baccharis* (Coquillett) (Goeden and Headrick 1991), *T. joanae* Goeden (Goeden 1993, 2001b), and *T. teerinki* Goeden (Goeden 2001c). The immature stages of a fifth species, *T. stigmatica* (Coquillett), will be described in my next paper, and its biology is relatively well known (Tauber and Toschi 1965; Goeden 1988a, 1993). This paper describes the life history, adults, and immature stages of the new species, *T. footei* Goeden, along with the adults of another new species, *T. headricki* Goeden, both segregates from the "*araneosa* complex" (Foote et al. 1993).

MATERIALS AND METHODS

The present study was based in part on specimens of adults belonging to the *araneosa* complex of *Tephritis* (Foote et al. 1993) reared from 1-liter samples of mature flower heads of various species of Asteraceae collected from throughout California since 1980 (Goeden 1993). The life history study and description of the immature stages of *T. footei* was based in large part on dissections of samples of mature and immature flower heads of *Artemisia tridentata* Nuttall (Asteraceae) collected north of the Hitchcock Ranch at the junction of U.S. Forest Service roads 3N16 and 3N54 in the San Bernardino National Forest (North Section) at 2,210-m elevation, southwestern San Bernardino Co., during 1995. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Two eggs, two first-, six second-, and nine third-instar larvae dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Sixteen arenas each consisting of a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994). Each arena contained a virgin male and female obtained from emergence cages that were used for observations of courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Format used to describe the adults follows the format and method of measurement of Jenkins and Turner (1989), as used and modified by Goeden (1993, 2001c). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c), Goeden et al. (1993), Goeden and Headrick (1991), Goeden and Teerink (1999), Teerink and Goeden (1999), and our earlier works cited therein. The holotypes and allotypes together with 74 and 25 reared paratypes of *T. footei* and *T. headricki*, respectively, have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The holotypes, allotypes, and 22 and 35 paratypes were used for measurements to describe *T. footei* and *T. headricki*, respectively. All remaining paratypes and voucher specimens not designated as paratypes, voucher specimens of immature stages, and reared parasitoids of *T. footei* reside in my research collections. Means ± SE are used throughout this paper. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 5.

RESULTS AND DISCUSSION

Taxonomy

The following key couplets modifying couplet 6 and replacing couplet 17 in the key of Foote et al. (1993), and replacing couplets 10 and 17 as previously modified by Goeden (1993, 2001c), enables one to distinguish these two new species. The three-digit, figure numbers in couplets 6, 10a, 18, and 19 refer to Foote et al. (1993), not to the present publication. The strike-throughs indicate parts of the original key that I suggest deleting.

6. Preapical brown area of wing interrupted by numerous round subhyaline spots (fig. 428, c); ~~dark pattern in cell r1 immediately posterior to pterostigma usually with at least 1 yellowish or hyaline spot (fig. 429, b); if no such spot present~~ anterior arm of Y-shaped mark at wing apex may be broken or conspicuously narrower than posterior arm (fig. 429, d) . . . 7

– Preapical brown area of wing usually with at most a few round subhyaline spots, its appearance never obscured by them (fig. 430, b); ~~dark pattern in cell r_1 immediately posterior to pterostigma unmarked (fig. 430, a);~~ Y-shaped mark in wing apex rarely broken as above 10

10. Anal lobe with dark markings of wing usually extending to wing margin 10a

– Anal lobe with dark markings of wing usually not, or only very faintly and narrowly, extending to wing margin 11

10a. Wing with hyaline spot in basal end of cell r_{4+5} large, oval to quadrate, and extended from vein R_{4+5} to vein M (often broadly based on the latter), usually contiguous with the hyaline area in cell r_{2+3} directly anterior to it; at least some of hyaline spots along margin of anal lobe wider than half the width of anal lobe; wing pattern as in Goeden (1993) . . . . *joanae* Goeden

– Wing with hyaline spot in basal end of cell cell r_{4+5} anterior to vein dm-cu, smaller, round or oval, and not extended from vein R_{4+5}, but sometimes touching vein M (fig. 430, c); hyaline spots along margin of anal lobe usually less than half the width of this lobe . . . . *signatipennis* Foote

17. Wing length of females usually under 2.6 mm; of males, usually under 2.3 mm (Fig. 1A) . . . . *footei* Goeden, n. sp.

– Wing length of females usually exceeding 2.6 mm; of males, usually exceeding 2.3 mm 18

18. Wing with hyaline spot in basal end of cell r_{4+5} large, oval to quadrate, and extending from vein R_{4+5} to vein M (often broadly based on the latter), usually contiguous with the hyaline area in cell r_{2+3} directly anterior to it (fig. 437) . . . . *araneosa* (Coquillett)

– Wing with circular, elliptical, ovate, or bell-shaped spot in cell r_{4+5} extending anteriorly from vein M, but usually not touching vein R_{4+5} 19

19. Femora, especially those of hind legs, dark tomentose; ~~frons reddish brown tomentose;~~ wing pattern as in fig. 438 . . *ovatipennis* Foote

– Femora all or mostly yellow~~; frons mostly white to yellow tomentose~~ 20

20. Oviscape two to three times as long as terminal abdominal tergite; hyaline spot in cell r_{4+5} anterior to vein dm-cu elliptical, oval, or bell-shaped and usually extending anteriorly from vein M more than two-thirds across cell r_{4+5}; wing pattern as in Goeden (2001c) . . . . *teerinki* Goeden

– Oviscape only slightly longer than the terminal abdominal tergite; hyaline spot in cell r_{4+5} anterior to vein dm-cu, smaller, round or oval, and may not touch vein M (Fig. 1B) . . . . *headricki* Goeden, n. sp.

Tephritis footei Goeden, new species
(Figs. 1A, 2–6)

Adult female.—*Head:* In profile, 1.1 to 1.3 times as high as long, face distinctly protruding below antennae, face and frons meeting at an angle of ca. 120°, gena below eye 0.18 to 0.24 times eye height, genal bristle and most genal setulae light brown; occiput slightly swollen; frons white to light yellow pollinose, white to greyish pollinose mid-dorsally and laterally, about 0.4 mm wide at vertex, narrowing to 0.3 mm at antennal bases, and 0.2 to 0.3 mm long; the two frontal setae dark brown to black; posterior orbital seta white, 0.4 to 0.7 times as long as anterior orbital seta; inner vertical seta dark brown, 0.5 to 0.7 times as long as head height, outer vertical bristle white, 0.2 to 0.3 times as long as head height; face, including antennal foveae, white; palpi and labellum light yellow to dark ocherous, sometimes tinged reddish, with four to seven, prominent, dark brown to black setulae apically; antenna 0.6 to 0.8 times as long as face at midline, yellow to dark ocherous, sometimes reddish, arista dark brown except base ocherous.

Thorax: Scutum, scutellum, and pleural

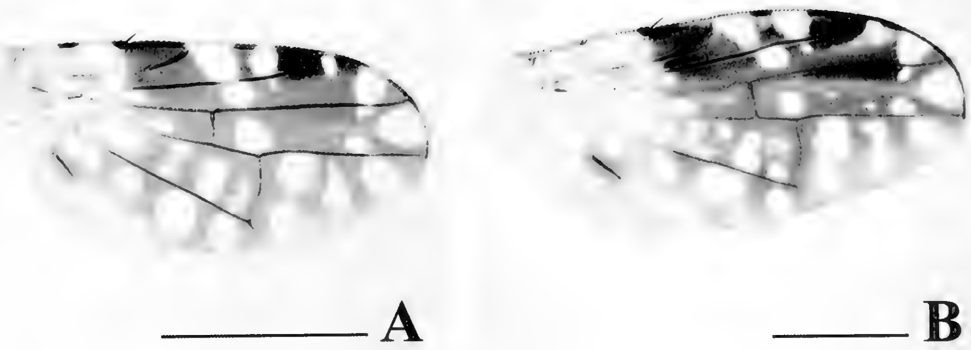

Fig. 1. (A) Right wing of *Tephritis footei* female; (B) Right wing of *T. headricki* female. Lines = 1 mm.

sclerites gray pollinose over shiny black ground-color, sometimes with single, slightly darker, faint, narrow, medial dorsolongitudinal stripe and faint lateral stripe through anterior dorsal central bristle; short, white setulae invest entire scutum; complement of thoracic bristles usual for the genus, all dark brown or black except posterior notopleural bristle, white; subscutellum and mediotergite black pollinose; scutellar setulae shorter and inserted closer to each other than are scutal setulae; scutellum bare centrally, setulae present only laterally; halteres yellow. Legs, especially femora, dark tomentose; hind tibia dark with parallel rows of black setulae; hind femur with black setulae on posterior sixth. Wing length 2.0–2.2 mm, wing pattern as in Fig. 1A, with a prominent hyaline area immediately distad of pterostigma extended from costal margin posterior to and touching vein R_{4+5}, but never extending to vein M; instead, usually round to oval, hyaline spot in basal end of cell r_{4+5} arising on and nearly always touching vein M, and usually extending at least halfway across cell r_{4+5}; dark area in pterostigma extending posteriorly to vein M and covering crossvein r-m, very rarely with hyaline markings; crossvein r-m removed from crossvein dm-cu by about its own length; large hyaline markings occupy most of cell m and extend posteriorly to posterior wing margin, as do large hyaline markings in cell cua_1, which do not cross vein CuA_1, but anteriorly divide into hyaline spots in cell dm; anal lobe mostly hyaline.

Abdomen: All tergites gray pollinose except T_6, which sometimes has shiny, black spot posteromedially, but otherwise is concolorous with mediotergite, other tergites without pattern; densely covered with colorless setulae inserted much closer to each other than their average length, becoming longer laterally and posteriorly; two or three long, hyaline to light or dark brown setae laterally along posterior margin of last abdominal tergite; oviscape flat, dark brown or black, with setulae on basal ⅔ similar to those on abdominal tergites, apical third with extremely fine, short black setae; oviscape in dorsal view 1.1 to 1.9 times as long as last abdominal tergite and 1.2 to 1.7 times as wide at base as long.

Male.—Similar to ♀ in all respects except wing length 1.7–2.1 mm; genitalia ocherous brown to black, subshining.

Variation.—Examination of reared *T. footei* with intact setation confirmed that the holotype, allotype, and most adults had two pairs of black frontal setae; however, one (1%) of 80 ♀ paratypes had five frontal setae, i.e., two pairs plus a third, weak, black seta inserted ventral to the other two pairs. One (1%) of 85 ♂ paratypes had three frontal setae, and another ♂ paratype had two pairs of frontal setae, one of which in the ventral pair was weak and white.

The right wings of the 80 ♀ paratypes varied from 1.7 to 2.6 mm in length, but 77 (96%) ♀ paratypes measured $\geq$ 1.8 and $\leq$ 2.4 mm; whereas, the right wings of the 85 ♂ paratypes varied from 1.7 to 2.3 mm in length.

Only one (1%) of the 80 ♀ paratypes had a single, faint, hyaline spot in cell r_1 within the dark area extending posteriorly from the stigma in one wing. Likewise, one (1%) of the 85 ♂ paratypes had one, faint, hyaline spot in cell r_{2+3} within this dark area in one wing.

The antennae of three (3.8%) of the 80 ♀ paratypes were tinged reddish, as were the first flagellomeres only of another 14 (17.5%) of the ♀ paratypes and the scape and peduncle of another ♀ paratype (1%). The labellum and palpi of four of these same 18 ♀ paratypes also were tinged reddish, as was the labellum alone of two more of these 18♀ paratypes, and the palpi of another one of the 18 ♀ paratypes. The antennae of four (4.9%) of the 85 ♂ paratypes were tinged reddish, as were the first flagellomeres only of one (1%) of the 85 ♂ paratypes and both the scape and peduncle of another (1%) ♂ paratype. The labellum and palpi of three of these same six ♂ paratypes also were tinged reddish, as was the labellum alone of the other three of these same six ♂ paratypes.

An additional four ♂ of the 85 ♂ paratypes examined bore the thalli of a benign, ectoparasitic fungus, *Stigmatomyces* sp. (Ascomycetes: Laboulbeniaceae), a genus reported from California by Goeden and Benjamin (1985).

Diagnosis.—The main morphological characters distinguishing the adults of *T. footei* from all other North American species north Mexico are its short wing length and the dark band in the wing extending obliquely from the pterostigma to cover vein r-m (Fig. 1A), which usually is free of hyaline spots. The wing length of *T. footei* is at least 1 mm shorter than that of *T. headricki* Goeden n. sp. described below, and the femora of *T. footei* are dark, not yellow like *T. headricki.* An elliptical, ovate, or bell-shaped, hyaline spot in cell r_{4+5} extending anteriorly from vein M, but not touching vein R_{4+5} (Fig. 1A), instead of a large oval to quadrate, hyaline spot in basal end of cell r_{4+5} extending from vein R_{4+5} to vein M (often broadly based on the latter), and usually contiguous with the hyaline area in cell r_{2+3} directly anterior to it, further distinguishes *T. footei* from the smallest specimens of *T. araneosa* (Coquillett).

The host relations of *T. footei, T. headricki,* and *T. araneosa* apparently also differ, as discussed in the next section. Indeed, as Foote et al. (1993) stated (p. 196), "... *araneosa* belongs to a complex of closely related species, the precise identification of which may never be attained without extensive biological studies." Foote (1960) described three of these, i.e., *candidipennis* Foote, *ovatipennis* Foote, *signatipennis* Foote, to distinguish those larger species with longer oviscapes, and Blanc (Foote and Blanc 1979) described another, *leavittensis* Blanc, on the basis of additional characters. Goeden (1993, 2001c) described *T. joanae* and *T. teerinki,* (respectively) two more of those *Tephritis* species with longer oviscapes. I also describe below in addition to *T. footei,* another new species with a shorter oviscape belonging to the "*araneosa* complex," i.e., *T. headricki.* Unfortunately, I have not been able to study its life history and immature stages, but am able to distinguish it morphologically, as noted above, as adults reared from a separate, different tribe of host plants in California.

Types.—Holotype: ♀; N(orth) of Hitchcock Ranch at 2,207-m (7,240-feet) (elevation), S(an) Bernardino Nat(ional) F(o)r(e)st, S(an) Bernardino Co(unty); T(ownship) 3N(orth), R(ange)1W(est), S(ection) 25; 27.x.1993; R. D. Goeden, coll. (hereafter RDG, coll.)/J. A. Teerink, coll. (hereafter JAT, coll.); reared from flower head of *Artemisia tridentata.* Allotype; ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 8 ♂ and 6♀; same data as holotype (5 ♂ and 5 ♀ to USNM). 1 ♀; same data as holotype, except 31.viii.1995; RDG/JAT, coll. (1 ♀ to USNM). 1 ♂ and 6 ♀; same data as holotype, except 13.ix.1995; RDG/JAT, coll. (3 ♀ to USNM). 3 ♂ and 2 ♀; same data as holotype, except 12.x.1995; RDG/JAT, coll. (1 ♂ and 1 ♀ to USNM). Unless otherwise indicated the following specimens also were reared from flower head of *A. tridentata.* 16 ♂ and 14 ♀; Onyx Summit at 8,370 ft (2,551 m), S. Bernardino Nat. Forest, S. Bernardino Co.; T1N, R3E, S12; 27.x.1993; RDG/JAT, coll. (6 ♂ and 6 ♀ to USNM). 6 ♂ and 4 ♀; St. Hwy. 38 N(orth)W(est) of Onyx Peak at 2,323 m (7,620 feet); S. Bernardino Nat. Frst., S. Bernardino Co.; T2N, R2E, S35; 27.x.1993; RDG/JAT, coll. (3 ♂ and 2 ♀ to USNM). 6 ♂ and 8 ♀; along road to Big Pine Flat (U. S. F(orest) S(ervice) Road 3N14) at 1,747 m (5,730 feet), S. Bernardino Nat. Forest, S. Bernardino Co.; T2N, R2W, S1; 27.x.1993; RDG/JAT, coll. (3 ♂ and 4 ♀ to USNM). 2 ♀; along road to Big Pine Flat (USFS Road 3N16) at 1,902 m (6,240 feet), S. Bernardino Nat. Forest., S. Bernardino Co., T2N, R1W, S6; 27.x.1993; RDG/JAT, coll. (1 ♀ to USNM). 17 ♂ and 12 ♀; E(ast) of Big Pine Flat Station (along) USFS Road 3N16 at 2,039 m (6,690 feet); S. Bernardino Nat. Forest., S. Bernardino Co., T5N, R1W, S29; 27.x.1933; RDG/JAT, coll. (7 ♂ and 4 ♀ to USNM). 4 ♂; same data as preceding entry, only all infected with *Stigmatomyces*; 9.viii.1995; (2 ♂ to USNM). 11 ♂ and 12 ♀; E(ast) of Big Pine Flat Station at 2,149 m (7,050 feet); S. Bernardino Nat. Forest, S. Bernardino Co., T5N, R1W, S28; 27.x.1993; RDG/JAT, coll. (6 ♂ and 6 ♀ to USNM). 6 ♂ and 5 ♀; Arrastre Flat at 2,225 m (7,300 feet); S. Bernardino Nat. Forest, S. Bernardino Co., T3N, R1E, S34; 27.x.1993; RDG/JAT, coll. (3 ♂ and 2 ♀ to USNM). 6 ♂ and 6 ♀; Junction (State) H(igh)w(a)y 38 and Heartbar R(oa)d (U. S. F(orest) S(ervice) Road 1N02) at 2,051 m (6,730 feet), S. Bernardino Nat. Forest, S. Bernardino Co.; T5N, R1W, S29; 27.x.1993; RDG/JAT, coll. (3 ♂ and 3 ♀ to USNM). 2 ♂ and 1 ♀; SE of Holcomb Valley Campground at 2,170 m (7,190 feet); S. Bernardino Nat. Forest, S. Bernardino Co., T2N, R1E, S4; 27.x.1933; RDG/JAT, coll. (1 ♂ to USNM). 1 ♂; Coon-creek Jumpoff at 2,192 m (7,190 feet); S. Bernardino Nat. Forest, S. Bernardino Co.; T1N, R2E, S22; 27.x.1993; RDG/JAT, coll. (1 ♂ to USNM).

Etymology.—This tephritid is named for an early mentor, Richard H. Foote, who encouraged my study of the nonfrugivorous Tephritidae of California, and whose many taxonomic writings provided examples of careful craftsmanship and a firm foundation and guidance for my own studies, especially those on *Tephritis* and *Trupanea* spp.

Tephritis headricki Goeden, new species
(Fig. 1B)

Adult female.—*Head:* In profile, 1.1 to 1.4 times as high as long, face distinctly protruding below antennae, face and frons meeting at an angle of ca. 120°, gena below eye 0.13 to 0.18 times eye height, genal bristle and most genal setulae light brown, some hyaline; occiput slightly swollen; frons white to ocherous pollinose, contrasting white to dark ocherous mid-dorsally and laterally, 0.5–0.6 mm wide at vertex, narrowing to about 0.4 mm at antennal bases, and 0.3 to 0.4 mm long; the two frontal setae dark brown to black; posterior orbital seta white, 0.6 to 0.8 times as long as brown anterior orbital seta; inner vertical seta brown, about 0.7 times as long as head height, outer vertical bristle white, 0.2 to 0.3 times as long as head height; face, including antennal foveae, white to reddish; palpus and labellum light yellow to dark ocherous, sometimes tinged reddish, with four to seven, prominent, brown setulae apically; antenna about 0.7 as long as face at midline, yellow to dark ocherous, sometimes reddish, arista brown except base ocherous.

Thorax: Scutum and pleural sclerites light-gray pollinose anteriorly, scutum darkening to golden brown pollinose posteriorly, all over shiny, dark brown to black ground-color; short, white setulae invest entire scutum; complement of thoracic bristles usual for the genus, all light to dark brown except posterior notopleural, white; scutellum golden brown medially, dark anteriorly along juncture with scutellum and dark apically, ocherous posteriolaterally, ventral half of subscutellum light-gray pollinose, dorsal half pale ocherous, mediotergite shiny black laterally and ventrally, dorsocentrally light-gray pollinose; scutellar setulae similar in length, but inserted closer to each other than scutal setulae; scutellum bare centrally, setulae present only laterally; halteres yellow, ocherous basally. Legs, yellow; hind tibia with parallel rows of brown setulae; hind femur with brown setulae on posterior fifth. Wing length 3.4 to 3.7 mm, wing pattern as in Fig. 1B, with a prominent hyaline area immediately distad of pterostigma extending from costal margin posterior to and touching vein R_{4+5}, with round to oval, hyaline spot in basal end of cell r_{4+5} just touching or slightly separated from vein M and usually only half or two-thirds as wide as cell r_{2+3} (Fig. 1B); dark area in pterostigma extending posteriorly to vein M and covering crossvein r-m, usually with no or one or two, faint to small, but discrete, hyaline spots in cell br; crossvein r-m removed from crossvein dm-cu by about its own length; large hyaline markings occupy most of cell m and extend posteriorly to posterior wing margin, as do large hyaline markings in cell cua_1, which may cross vein CuA_1, or occupy as separate hyaline spots, most of cell dm; anal lobe usually hyaline along wing margin or occasionally very faintly patterned with large, hyaline spots.

Abdomen: All tergites light-gray pollinose, concolorous with dorsocentral part of mediotergite, without pattern; densely covered with colorless setulae inserted much closer to each other than their average length, becoming longer laterally and posteriorly; two or three, long, hyaline to light or dark brown setae along posterior margin of last abdominal tergite; oviscape flat, dark-brown to black, with setulae on basal ⅔ similar to those on abdominal tergites, apical third with extremely fine, short dark brown setae; oviscape in dorsal view 1.2 to 1.8 times as long as last abdominal tergite and 1.2 to 1.9 as wide at base as long.

Male.—Similar to ♀ in most respects except wing length 3.0–3.6 mm; genitalia ocherous to dark brown, subshining.

Variation.—Examination of reared *T. headricki* with intact setation confirmed that the holotype, allotype, and all paratypes except one ♀ had two pairs of black frontal setae; this female had a third pair of short, white setae between the other two pairs of frontal setae.

Eight (50%) of the 16 ♀ types had no hyaline spot, however faint, in cells r_1, r_{2+3}, or br within the dark area extending posteriorly from the stigma in both wings. Two (13%) of the 16 ♀ types had one faint hyaline spot in cell r_{2+3} within this dark area in only one wing. Eight (50%) of the 16 ♀ types had one or two, faint to small, but discrete, hyaline spots in the apex of cell br, basad of crossvein r-m. In comparison, eight (35%) of 22 ♂ types had no hyaline spot, however faint, in cells r_1, r_{2+3}, or br within the dark area extending posteriorly from the stigma. Only one (5%) of the 22 ♂ types had one, small, discrete and two, faint hyaline spots in cell r_{2+3} within each dark area, respectively, in its wings. And, 15 (68%) of the 22 ♂ types had one or two, faint to prominent, hyaline spots in the dark area at the apex of cell br, basad of crossvein r-m.

The hyaline spot in the basal end of cell r_{4+5} reaches vein M posteriorly in seven (44%) of 16 ♀ types, but was slightly separated from vein M in the remaining nine (56%) 16 ♀ types. Likewise, the hyaline spot in the basal end of cell r_{4+5} reaches vein M posteriorly in 13 (59%) of 22 ♂ types, but was slightly separated from vein M in another eight (36%) of 22 ♂ types. The one remaining ♂ type had one wing in each category.

The anal lobe of only one (6%) of the 16 ♀ types contained a very faint pattern with large hyaline spots that extended to and along the wing margin; whereas, three (14%) of the 22 ♂ types showed this condition.

The first flagellomeres of the antennae of nine (56%) of 16 ♀ types were tinged reddish, as were both pedicels of still another (6%) of the ♀ types. The labellum and palpus of three of these same 10 ♀ types also were tinged reddish, as was the labellum or palpi alone of two other, separate ♀ paratypes. The antennae of four (18%) of the 22 ♂ types were tinged reddish, as were the first flagellomeres only or pedicels only of another two each (9 and 9%) of the 22 ♂ types. The labellum and palpus of 10 (45%) of these 22 ♂ types also were tinged reddish, as was the labellum alone or palpi alone of one each (5 and 5%) of these 22 ♂ types. As some, but not all specimens of *T. araneosa* and *T. ovatipennis* (unpublished data) as well as *T. footei* and *T. headricki* had reddish colored head parts, this character is removed from couplet 19a describing *T. ovatipennis* in my revision above of the key to *Tephritis* in Foote et al. (1993). This reddish coloration apparently lies on a continuum of colorations from white to yellow to ocherous to reddish to brown to black seen in *Tephritis*.

Diagnosis.—The main morphological characters distinguishing the adults of *T. headricki* from all other North American species of *Tephritis* north Mexico are a combination of a round or ovate, hyaline spot in cell r_{4+5} anteriorad of vein M, and not touching vein R_{4+5} (Fig. 1B); the dark band from pterostigma to vein M extending obliquely to cover vein r-m (Fig. 1B); yellow femora; and an oviscape only about twice as long as the last abdominal tergite. The femora of *T. ovatipennis*, especially those of the hind legs are dark grey to black tomentose, not yellow (Foote et al. 1993). Moreover, *T. ovatipennis* and *T. teerinki* belong to those larger congeners in the "*araneosa* complex" (Foote 1960, Foote et al. 1993) with long oviscapes, not like those of *T. araneosa* with an oviscape "... only slightly longer or shorter than, or equal to, the terminal abdominal tergite ...". In this last regard, of 62 *T. araneosa* reared from four species of *Artemisia* other than *A. tridentata* (see discussion of hosts below), none had oviscapes shorter than the terminal abdominal tergite, only one (5%) was equal, and the remainder had oviscapes from 1.1 to 1.7 times as long as the terminal abdominal tergite. Another grouping of 104 *T. araneosa* reared from three *Chrysothamnus* spp. and one *Ericameria* spp. (which I could not distinguish morphologically as another new species; see discussion of hosts below) also contained none with an oviscape shorter than or equal to the terminal abdominal tergite. The oviscapes of these 104 females varied from 1.1 to 2.3 times as long as the terminal abdominal tergites. No obvious distinctions in measurements or perceived characters of these two groups could be correlated with their distinctive host-plant taxonomic affinities. These two groups represent what remains of *T. araneosa* after the removal of segregates with longer oviscapes by Foote (1960), Foote and Blanc 1979), and Goeden (1993, 2001c), and two more species with shorter oviscapes in the present paper. This "residual" *T. araneosa* probably contains at least one more undescribed species.

Types.—Holotype: ♀; Dead Man Creek at 2,500 m (elevation), Inyo National Forest, Mono County; T(ownship)3S(outh), R(ange)27E(ast), S(ection)5; 9.x.1986; R. D. Goeden, coll. (hereafter RDG, coll.); reared from flower head of *Solidago canadensis* L. Allotype: ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 8 ♂ and 8♀; same data as holotype (5 ♂ and 5 ♀ to USNM). 7 ♂ and 5 ♀; Beasore Meadow off Beasore Road 25 km N(orth)E(ast) of Bass L(ake) at 1,960 m, Sierra National Forest, Madera County; T6S, R23E, S5; 16.ix.1988; RDG, coll.; reared from flower heads of *S. canadensis* (4 ♂ and 3 ♀ to USNM). 2 ♀; along Upper Deadman Creek at 2,496 m; Inyo National Forest, Mono County; T3S, R27E, S6;

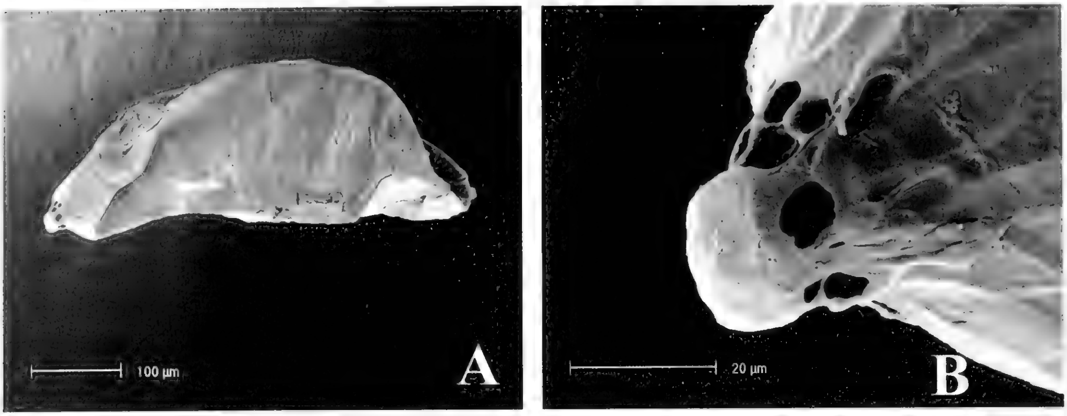

Fig. 2. Egg of *Tephritis footei:* (A) habitus, anterior to left; (B) pedicel showing pattern and shapes of aeropyles.

18.ix.1991; RDG/JAT, coll.; reared from flower heads of *S. canadensis* (1 ♀ to USNM). 4 ♂; Antelope Spring; Inyo National Forest., Inyo County; T17S, R35E, S24; 15.ix.1982; RDG, coll.; reared from flower head of *S. confinis* Nuttall (2 ♂ to USNM). 1 ♂; Kennedy Meadows, Sequoia National Forest; Inyo County; T22S, R35E, S24; 25.ix.1980; RDG, coll.; reared from flower head of *Euthamia* (formerly *Solidago*) *occidentalis* Nuttall (1 ♂ to USNM). 1 ♂; Round Valley Reservoir at 1,372 m; Plumas National Forest; Plumas County; 10.ix.1986; RDG, coll.; reared from flower head of *E. occidentalis* (1 ♂ to USNM).

Etymology.—*Tephritis headricki* is named for my friend, last Ph.D. student, and research collaborator, David H. Headrick, who as my successor in California tephritidology hopefully will one day study and publish the life history and describe the immature stages of his tephritid namesake.

Immature stages.—The egg, first-, second-, and third-instar larvae of *Tephritis footei* are described below.

Egg.: Five eggs measured *in situ* in field-collected, preblossom flower heads plus a total of five ova dissected from two females were white, opaque, smooth, elongate-ellipsoidal, 0.52 ± 0.007 (range, 0.48–0.56) mm long, 0.16 ± 0.005 (range, 0.14–0.18) mm wide, smoothly rounded at tapered basal end (Fig. 2A); pedicel button-like, 0.02 mm long, circumscribed apically by different-sized, semicircular aeropyles arranged singly or in rows of two parallel to the long axis of the egg (Fig. 2B).

The egg of *T. footei* (Fig. 2A), like those of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), differs from eggs of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993) by lacking prominent polygonal reticulation of the chorion. Also, the egg of *T. footei,* like those of *T. teerinki* and *T. joanae,* apparently is covered by a smooth, membraneous sheath (Figs. 2A, B; Goeden 2001b, c), which remains intact and is not partly shed and peeled back during oviposition as in the other two species. The function of this membraneous sheath remains unknown. It was first reported for *T. arizonaensis* by Goeden et al. (1993), who then belatedly recognized it in *T. baccharis,* and apparently it only has been reported to date from the eggs of these five species of *Tephritis.* In *T. arizonaensis* (Goeden et al. 1993), this membraneous sheath also is prominently, longitudinally striated. Weak longitudinal striations are present at the anterior, pedicellar end of the egg of *T. footei* (Figs. 2A, B), but otherwise are not seen on the rest of the egg body.

First instar larva: White, cylindrical (Fig. 3A); gnathocephalon conical; dorsal sensory organ well-defined, round, flattened (Fig. 3B-1); anterior sensory lobe (Fig. 3B-2) with ter-

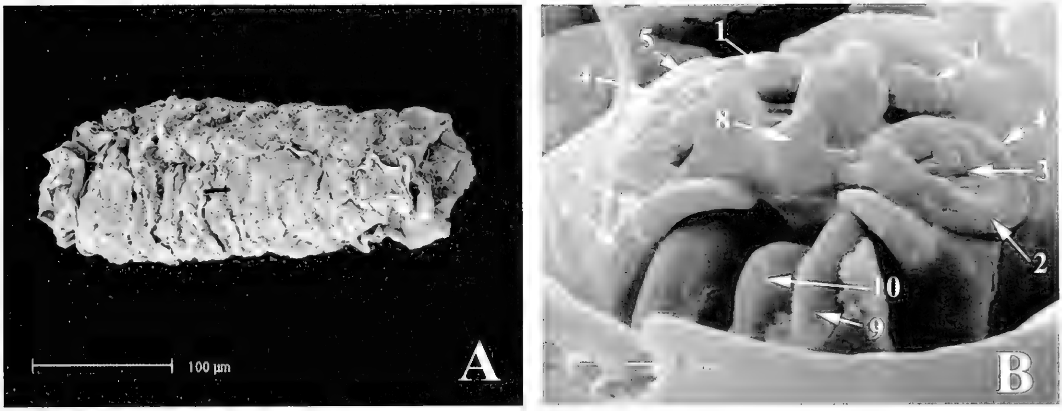

Fig. 3. First instar of *Tephritis footei:* (A) habitus, anterior to left; (B) gnathocephalon, ventrofrontal view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ, 7—"lateral" integumental petal, 8—"median" integumental petal, 9—mouthhook, 10—median oral lobe.

minal sensory organ (Fig. 3B-3), lateral sensory organ (Fig. 3B-4), supralateral sensory organ (Fig. 3B-5), and pit sensory organ not seen; stomal sense organ (Fig. 3B-6) ventrolaterad of anterior sensory lobe and fused with flattened, protrudent, "lateral" integumental petal (Fig. 3B-7) dorsad of each mouthhook, one "median" integumental petal between anterior sensory lobes (Fig. 3B-8); mouthhook (Fig. 3B-9) bidentate (not shown); median oral lobe laterally compressed, apically rounded (Fig. 3B-10). Remaining characters could not be seen on the few specimens examined.

Only the first instar of *T. teerinki* has been described in detail (Goeden 2001c) for which this partial description for *T. footei* provides at least some basis for comparison. For example, it is worth noting that an integumental petal fused with the stomal sense organ (Figs. 3B-6, -7) also distinguished the first instar of *T. teerinki* (Goeden 2001c) and the first instars of at least five species of *Neaspilota* (Goeden 2001a) from subsequent instars. This character was first reported for the first instar of *Trupanea vicina* (Wulp) (Goeden and Teerink 1999).

Second instar larva: White, cylindrical, rounded anteriorly, truncated posteriorly, body segments well-defined (Fig. 4A); gnathocephalon not seen; anterior thoracic spiracle with five, subglobose or subquadrate papillae (Fig. 4B); lateral spiracular complexes not seen; posterior spiracular plate bears three ovoid rimae (Fig. 4C-1), ca. 0.02 mm long, and four interspiracular processes (Fig. 4C-2), each with one or two, lanceolate branches, each with one or two apical teeth, longest branch measuring 0.01 mm; stelex sensillum ventrolaterad (Figs. 4C-3, D-1) of posterior spiracular plate, dorsolateral stelex sensillum observed, but not shown; no other sensillum seen at lateral position; intermediate sensory complexes (Fig. 4D-2) with a stelex sensillum (Fig. 4D-3) and a medusoid sensillum (Fig. 4D-4).

The habitus of the second instar of *T. footei* (Fig. 4A) approximates those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c). Again, the partial description for *T. footei* allowed limited comparison with the second instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), the only species described in sufficient detail to date to allow full comparison of characters. The anterior spiracle of second instar *T. footei* bears five, subglobose or subquadrate papillae (Fig. 4B), like that of *T. joanae* (Goeden 2001b), not four, doliform papillae like *T. teerinki* (Goeden 2001c). Only minor differences in

Fig. 4. Second instar of *Tephritis footei:* (A) habitus, anterior to right; (B) anterior spiracle; (C) caudal segment, 1—rimae, 2—interspiracular processes, 3—ventrolateral stelex sensillum; (D) 1—ventrolateral stelex sensillum, 2—intermediate sensory complex, with 3—stelex sensillum and 4—medusoid sensillum.

the number of branches on the interspiracular processes, i.e., one to two for *T. footei* (Fig. 4C-2), one to three for *T. teerinki* (Goeden 2001c), versus two to four for *T. joanae* (Goeden 2001b), were noted. Also, the branches of the interspiracular processes of *T. footei* are lanceolate (Fig. 4C-2), not foliose, like those of the second instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c).

Third instar larva: White, ellipsoidal, distinctly segmented, tapered anteriorly, truncated posteriorly (Fig. 5A); gnathocephalon conical, anteriorly flattened, and medially divided by a vertical suture (Fig. 5B-1); posteriorly directed, spinose, minute acanthae incompletely circumscribe prothorax anteriorly (Figs. 5B-2, C-12), instead many round to elongate-rounded, integumental petals circumscribe central half of prothorax (Fig. 5B-3); dorsal sensory organ well-defined, hemispherical (Fig. 5C-1); anterior sensory lobe (Fig. 5C-2) bears terminal sensory organ (Fig. 5C-3), lateral sensory organ (Fig. 5C-4), supralateral sensory organ (Fig. 5C-5), and pit sensory organ (Fig. 5C-6); two medial, papilliform integumental petals (Fig. 5C-7) and two, lateral, spatulate, integumental petals (Fig. 5C-8) in two rows above each mouthhook (Fig. 5C-9), lower lateral petal continuing laterally around oral cavity, and separate from stomal sense organ (Fig. 5C-10) ventrolaterad of anterior sensory lobe; at least three complete oral ridges (Fig. 5C-11) laterad of each anterior sensory lobe; mouthhook apparently bidentate; median oral lobe

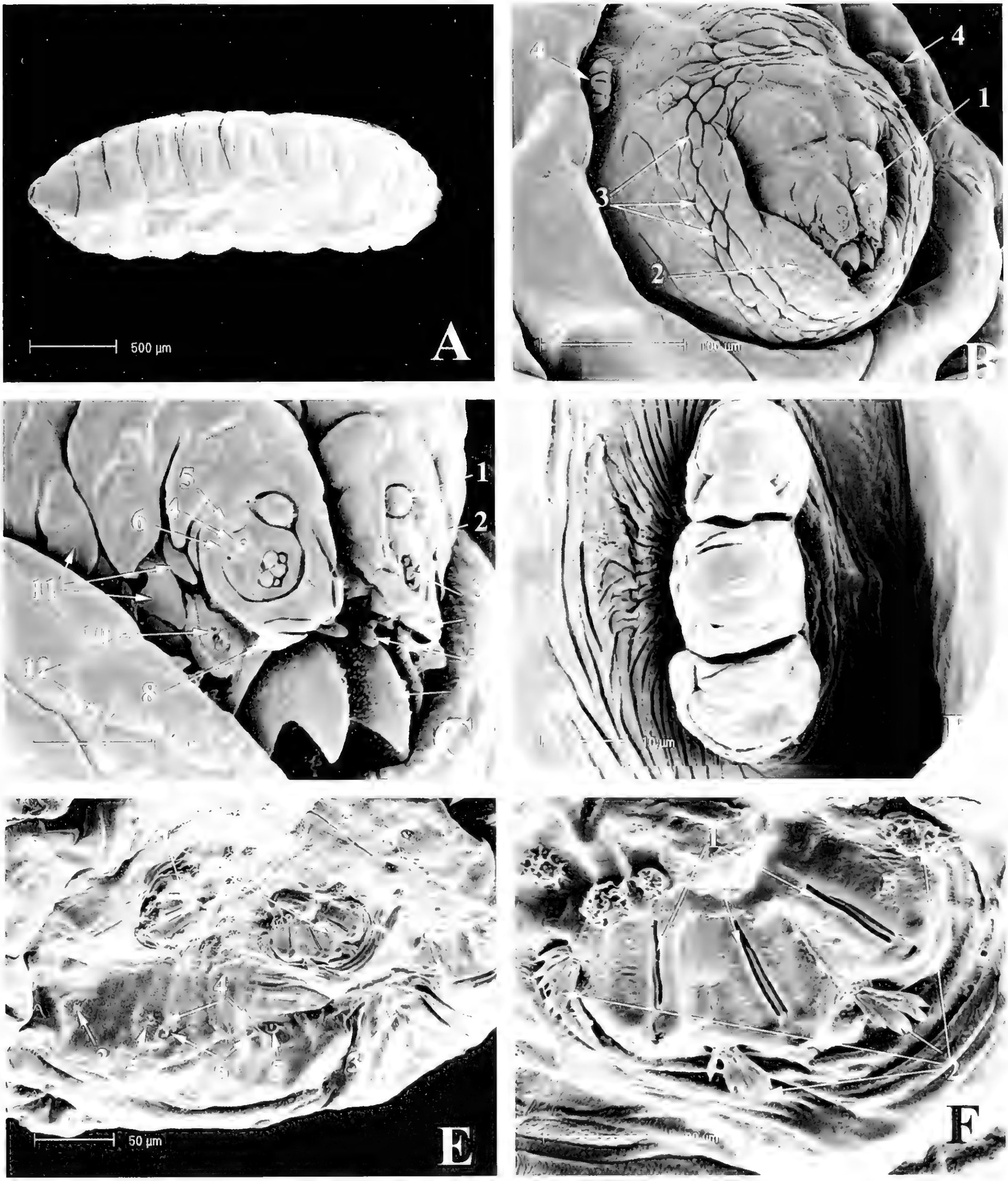

Fig. 5. Third instar of *Tephritis footei:* (A) habitus, anterior to left; (B) gnathocephalon and prothorax, frontolateral view, 1—vertical medial suture of gnathocephalon, 2—minute acanthae, 3—integumental petals on prothorax, 4—anterior spiracle; (C) gnathocephalon, frontolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—medial integumental petal, 8—lateral integumental petal, 9—mouthhook, 10—stomal sense organ, 11—oral ridges, 12—minute acanthae; (D) anterior spiracle; (E) caudal segment, 1—spiracular plates, 2—dorsolateral stelex sensillum, 3—ventrolateral stelex sensillum; 4—intermediate sensory complex, with 5—stelex sensilla and 6—medusoid sensillum; (F) posterior spiracular plate, 1—rimae, 2—interspiracular processes.

present, but only partially seen and not pictured; anterior thoracic spiracle on posterior margin of prothorax bears three (not shown) or four subglobose or subquadrate papillae (Figs. 5B-4, 5D); mesothoracic, metathoracic, and abdominal lateral spiracular complexes not seen; each posterior spiracular plate (Fig. 5E-1) surrounded by a pair of dorsolateral stelex sensilla (Fig. 5E-2) and ventrolateral pair of stelex sensilla (Fig. 5E-3); each posterior spiracular plate bears three ovoid rimae (Fig. 5F-1), ca. 0.02 mm in length, and four, three- to four-branched, single-, bi- or trifurcately-tipped, interspiracular processes, each ca. 0.05 mm long (Fig. 5F-2); intermediate sensory complex (Fig. 5E-4) with a stelex sensillum (Fig. 5E-5) and a medusoid sensillum (Fig. 5E-6).

The habitus of the third instar of *T. footei* differs from those of four other described congeners in at least two ways. The elongate-ellipsoidal shape of the third instar of *T. footei* (Fig. 5A) appears intermediate to the ovoidal shape of the third instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c) and the cylindrical shape ascribed to third instars of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). The prothorax (Fig. 5B-1) is circumscribed by many more integumental petals than the much smoother prothoracic segments of the four other species of *Tephritis* examined to date (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c). Fewer minute acanthae anteriorly circumscribe the prothorax of the third instar of *T. footei* (Fig. 5B-2) than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c). On the other hand the gnathocephalon, or at least the anterior sensory lobes of all five species are separated by a vertical medial suture (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c; Fig. 5B).

The integumental petals in the third instars of all five congeners examined to date are arranged in a double row above each mouthhook, but those of *T. footei* (Fig. 5C-8) occur in two rows of two like *T. teerinki* (Goeden 2001c), with an additional, medial pair of different shape in *T. footei* (Fig. 5C-7). However, the integumental petals of both *T. teerinki* (Goeden 2001c) and *T. footei* (Figs. 5C-7, 8) are fewer in number than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b). Both *T. footei* and *T. teerinki* also apparently lack the additional integumental petals found in a vertical double row above these papillae, one pair to each side of the medial depression separating the anterior sensory lobes (Fig. 5C-2; Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c). The integumental petals increase in number between the last two instars of *T. footei* (Figs. 5C-7, 8), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c).

The mouthhooks of the third instars of *T. footei* (Fig. 5C-9), like those of *T. teerinki* (Goeden 2001c), appear bidentate, unlike the tridentate mouthhooks of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b). However, most of the nine specimens of third instar *T. footei* examined by SEM had their mouthparts hidden, which precluded examination of the oral cavity and mouthhooks in ventral view.

The anterior spiracle of the third instar of *T. footei* (Fig. 5D) bore three or four papillae, one or two less than the second instar, but not three in the second instar and three or four in the third instar, like *T. joanae* (Goeden 2001b), or four in the second instar and five in the third instar as reported for *T. teerinki* (Goeden 2001c).

Goeden (2001c) discussed the stelex sensilla surrounding the posterior spiracular plates of the third instars that apparently differ in number among the *Tephritis* species examined to date. However, the caudal segment of the third instar of *T. footei,* like those of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), apparently are surrounded by a dorsolateral and ventrolateral pair of stelex sensilla (Figs. 5E-2, 3) as well as a ventral pair of intermediate spiracular complexes

(Fig. 5E-4), the medusoid sensilla of each bears short apical papillae typical of this type of chemosensillum (Goeden 2001a, b, c; Goeden and Teerink 1999, and references therein).

Puparia: All puparia prepared for SEM unfortunately turned out to be *Campiglossa clathrata* (Loew), which imperfectly, temporally partitions and thus shares the flower heads of *A. tridentata* with *T. footei,* i.e., symphagy (Goeden 1997). Other puparia examined, identified, and measured *in situ* provided the basis for the following abbreviated description.

Dull black, ellipsoidal, and smoothly rounded at both ends. Thirty-four puparia averaged 1.87 ± 0.02 (range, 1.63–2.13) mm in length; 0.98 ± 0.013 (range, 0.85–1.14) mm in width.

DISTRIBUTION AND HOSTS

To date, *Tephritis footei* is only known from California and from flower heads of *Artemisia tridentata*; however, it has been reported elsewhere by me (Goeden 1993), and probably by others, as *T. ovatipennis,* and this should be corrected. Accordingly, *T. footei,* possibly may be a nearly monophagous, widely distributed species on *A. tridentata,* which itself is widely distributed throughout the western United States (Hickman 1993), and belongs to the subtribe Artemisiinae of the Tribe Anthemideae (Bremer 1994). This monophagy is presumed because *T. araneosa,* as now constituted, has been reared from flower heads of four other California species of *Artemisia,* i.e., *A. californica* Lessing, *A. douglasiana* Besser, *A. dracunculus* L., and *A. ludoviciana* Nuttall, the last-named plant formerly was reported as a host of *T. ovatipennis* by Goeden (1993), which now should be deleted; whereas, *A. dracunculus* is a new host record for *T. araneosa* (Goeden 1993). As noted above, *T. araneosa,* or what is probably a separate new species near *araneosa,* also has been reared by me from *Chrysothamnus nauseosus* (Pallas) Britton, *C. parryi* (A. Gray) E. Greene, *C. teretifolius* (Durand and Hilgard) H. M. Hall, *C. viscidiflorus* (Hooker) Nuttall, and *Ericameria* (as *Haplopappus) bloomeri* (A. Gray) J. F. Mcbride, most of which were reported as hosts of *T. araneosa* by Goeden (1993), except for this newly confirmed host record for *C. nauseosus* in Wasbauer (1972). *Chrysothamnus* and *Ericameria* both belong to the subtribe Solidagininae of the tribe Astereae (Bremer 1994). Also as noted above, *T. headricki* is an oligophagous tephritid, reared solely from the flower heads of two species of *Solidago,* i.e., *S. canadensis* and *S. confinis* and *Euthamia occidentalis,* all three of which belong to the subtribe Solidagininae of the tribe Astereae (Bremer 1994). The first two plant species were reported as hosts of *T. ovatipennis* by Goeden (1993), which now need to be deleted, and the latter plant represents a new host-plant genus and species record for *Tephritis. Tephritis headricki* undoubtedly has additional hosts as yet undiscovered, and probably is a widespread species like its widespread and diverse host-plant genus, *Solidago* (Hickman 1993). Goeden (2001c) also removed *Hulsea* spp. from those hosts reported by Goeden (1993) as *T. ovatipennis,* when he described *T. teerinki.* The three specimens identified and reported by Goeden (1993) for *T. ovatipennis* reared from *Machaeranthera canescens* (Pursh) A. Gray, upon re-examination were re-identified and confirmed with other reared specimens as *T. michiganesis* Quisenberry; this finding extends its distribution across the western United States to southern California from western Minnesota/eastern North Dakota, and represents the first host-plant record for this tephritid (Foote et al. 1993). Therefore, as presently constituted, *T. ovatipennis* represents an oligophagous species reared from two species of *Erigeron,* i.e., *E. foliosus* Nuttall and *E. glaucus* Ker-Gawler, and *Trimorpha lonchophyllus* (Hooker) G. Nesom, all of which belong to the subtribe Asterinae of the tribe Astereae. Of the last three species, the first named is a new host-plant record; the second and third species were reported as hosts of *T. ovatipennis* by Goeden (1993), the third also as another species of *Erigeron* (Hickman, 1993). Recent revisions by plant and insect taxonomists (Hickman 1993; Bremer 1994; Goeden 2001a, b) have helped to clarify and better interpret the host affinities of these California *Tephritis* since Goeden (1993), but continued study is needed of these and other *Tephritis* belonging or not to the "*araneosa* complex."

BIOLOGY

Egg.—In each of 11, closed, preblossom, immature flower heads of *Artemisia tridentata* a single egg of *T. footei* was inserted pedicel-last through one or more phyllaries into an ovule (Fig. 6A). Thus, the 11 eggs each rested with their long axes at a 45° to 60° angle to the receptacles of the young flower heads and an average of one ovule/floret was damaged per flower head by oviposition. Thus, about 25% of an average total of 4.3 ± 0.2 (range, 3–7) ovules/florets counted in 27 infested, closed preblossom flower heads were damaged by oviposition. The receptacles of preblossom heads that contained eggs averaged 0.36 ± 0.02 (range, 0.28–0.4) mm in diameter.

Larva.—Upon eclosion, the single first instars found feeding in seven, closed, preblossom flower heads tunneled immediately into a floret and then continued to feed parallel to the receptacle on one or more ovules (Fig. 6B). The receptacles of these seven infested flower heads averaged 0.39 ± 0.02 (range, 0.28–0.46) mm in diameter and an average of 1.8 ± 0.49 (range, 1–3) ovules was damaged in these seven flower heads. No receptacle was abraded or pitted by larval feeding. Thus, about 42% (range, 25–70%) of an average total of 4.3 ovules/florets counted for the above-mentioned, 27 flower heads were damaged by the first instars.

Second instars (Fig. 6C) continued feeding on ovules in closed, preblossom flower heads. They fed with their bodies perpendicular to the receptacles, but always well above the receptacles (Fig. 6C). Receptacles of 25 flower heads containing second instars averaged 4.30 ± 0.22 (range, 2.28–6.84) mm in diameter. These eight flower heads each contained a single larva that had damaged a single ovule, or again, about 25% of the average total of 4.3 ovules/florets per flower head counted within the above-mentioned, 27 flower heads.

Third instars in flower heads fed with their long axes oriented perpendicular to the receptacles, and with their mouthparts commonly directed towards (Fig. 6D), or less commonly, away from the receptacles (Fig. 6E). All of the ovules/florets in each of the heads were destroyed (Figs. 6D, E). The receptacles were abraded or pitted in two (64%) of nine, closed flower heads containing third instars, or the larvae were found feeding on the basal fragments of the ovules connected to the receptacles, which suggested that sap constituted at least part of the diet of third instars of *T. footei,* probably towards the end of the third stadium. Goeden (1988b), Headrick and Goeden (1990), Goeden and Headrick (1992), Goeden et al. (1993, 1995), Headrick et al. (1996), Goeden and Teerink (1997) first noted, described, and discussed sap feeding by florivorous species of Tephritidae in the genera *Trupanea, Paracantha, Neaspilota, Tephritis, Urophora, Dioxyna,* and *Xenochaeta,* respectively. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed puparia (Fig. 6F).

Pupa.—The receptacles of 43 flower heads, each of which contained a single puparium (Fig. 6F) averaged 0.6 ± 0.04 (range, 0.42–1.42) mm in diameter. The receptacles were abraded or pitted in 19 of 43 (44%) flower heads containing puparia, further confirming that sap constituted part of the diet of the third instars. All of the contents of these flower heads were destroyed and the puparia occupied most of the flower heads (Fig. 6F).

Adult.—Adults (Fig. 6G, H) apparently are long-lived and constitute the only overwintering stage in southern California. Under insectary conditions, six unmated females (Fig. 6G) lived an average of 87 ± 8 (range, 71–120) days, and five virgin males (Fig. 6H) averaged 64 ± 12 (range, 18–91) days. Such

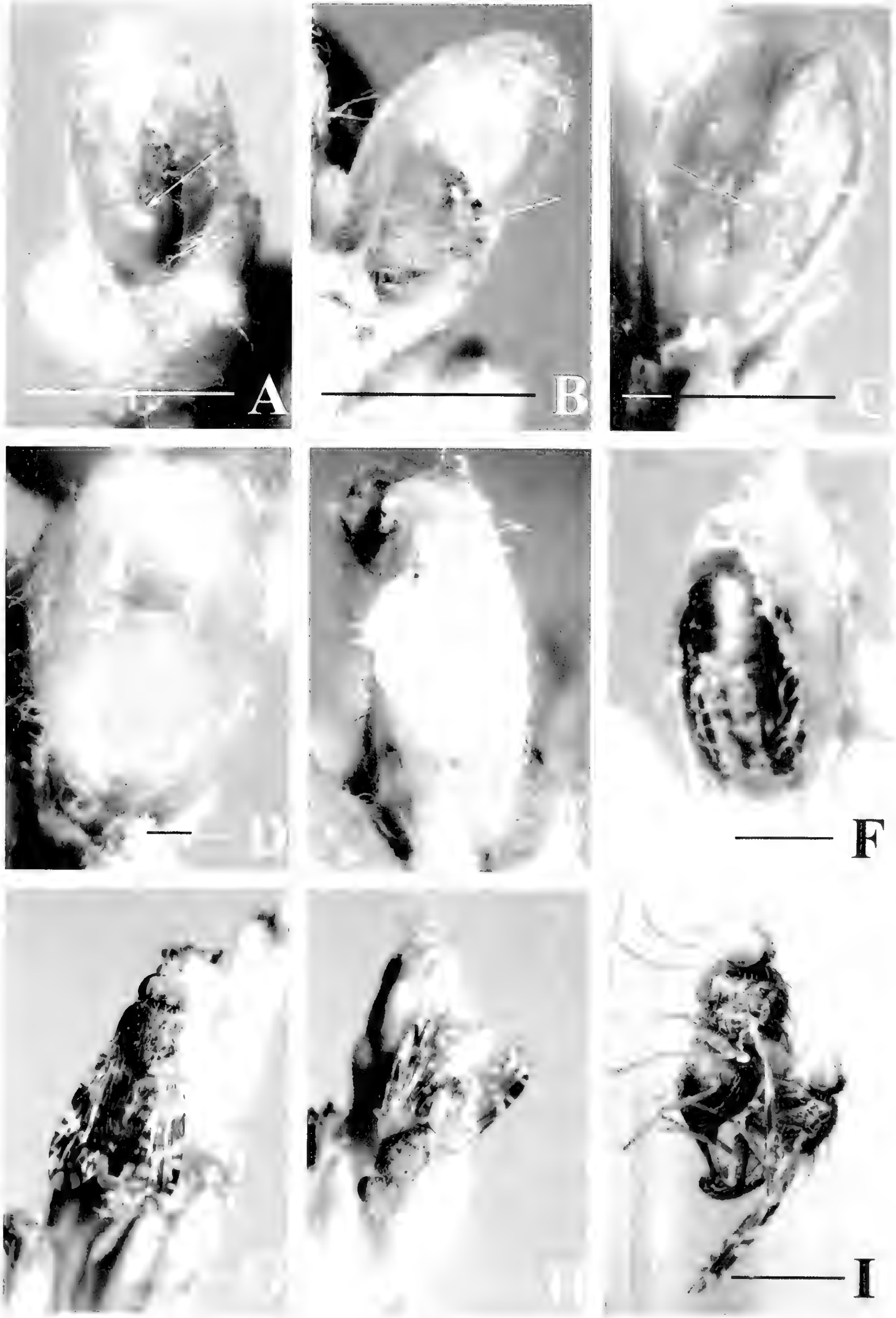

Fig. 6. Life stages of *Tephritis footei* in flower heads of *Artemisia tridentata:* (A) egg (arrow) in closed, preblossom flower head inserted into floret; (B) first instar (arrow) feeding within floret in preblossom flower head; (C) second instar (arrow) feeding in adjacent florets in preblossom flower head; (D) third instar feeding on receptacle in closed, preblossom flower head; (E) full-size, third instar positioned for pupariation; (F) single puparium occupying interior of flower head; (G) adult female; (H) adult male; (I) mating pair with female forming droplet. Lines = 1 mm.

lengthy longevities are commensurate with the aggregative type of life history possessed by this tephritid (Headrick and Goeden 1994, 1998).

The premating and mating behaviors of *T. footei* were not studied in the field, but were limitedly observed in petri dish arenas of the type otherwise found to be so useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors occasionally observed with *T. footei* were tracking and side-stepping by males (Headrick and Goeden 1994). The most common wing display was asynchronous supination by both sexes, both spontaneous and in response to other individuals (Goeden et al. 1993; Headrick and Goeden 1994, 1999). Males did not exhibit any of the common tephritid courtship displays, including regular, abdominal pleural distension. Four pairs were observed to mate (Fig. 6I) once or twice per day for a total of 10 matings that lasted an average of 208 (range, 84–316) min. Copulatory induction behavior (CIB) (Headrick and Goeden 1994, 1999), and the copulatory positions attained by each sex, generally were as described for *T. arizonaensis* (Goeden et al. 1993). Separation of a male and female was observed three times, with the male turning and rapidly walking off and away from the female while pulling free his genitalia.

Seasonal history.—The life cycle of *T. footei* on *Artemisia tridentata* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the adult is the principal overwintering stage. Consequently, come late-spring/early summer (May to June), adults aggregate on preblossom shoots and subsequently oviposit in the small, newly-formed, closed, preblossom flower heads. The larvae feed until fully grown, then pupariate in flower heads and emerge in midsummer (late-June to July). They spend the rest of the summer and fall, probably as non-reproductive adults, feeding in mountain meadows and riparian habits where they subsequently overwinter. Or, possibly two overlapping, nondescrete generations are produced starting earlier on lower-elevation, or later on higher-elevation, host plants.

Natural enemies.—*Halticoptera* sp. and *Mesopolobus* sp. (Hymenoptera: Pteromalidae) were reared from separate puparia of *T. footei* as solitary, larval-pupal endoparasitoids. Many additional specimens of both species were reared from caged mature flower heads of *A. tridentata* as probable parasitoids.

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GEOICA SETULOSA (PASSERINI) (HEMIPTERA: APHIDIDAE): NEW DISTRIBUTION RECORDS FOR NORTH AMERICA

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Abstract.—We report the first eastern United States records of the fordine aphid *Geoica setulosa* (Passerini). Description and illustrations of the apterous viviparous female and a key to species of *Geoica* in the United States are provided.

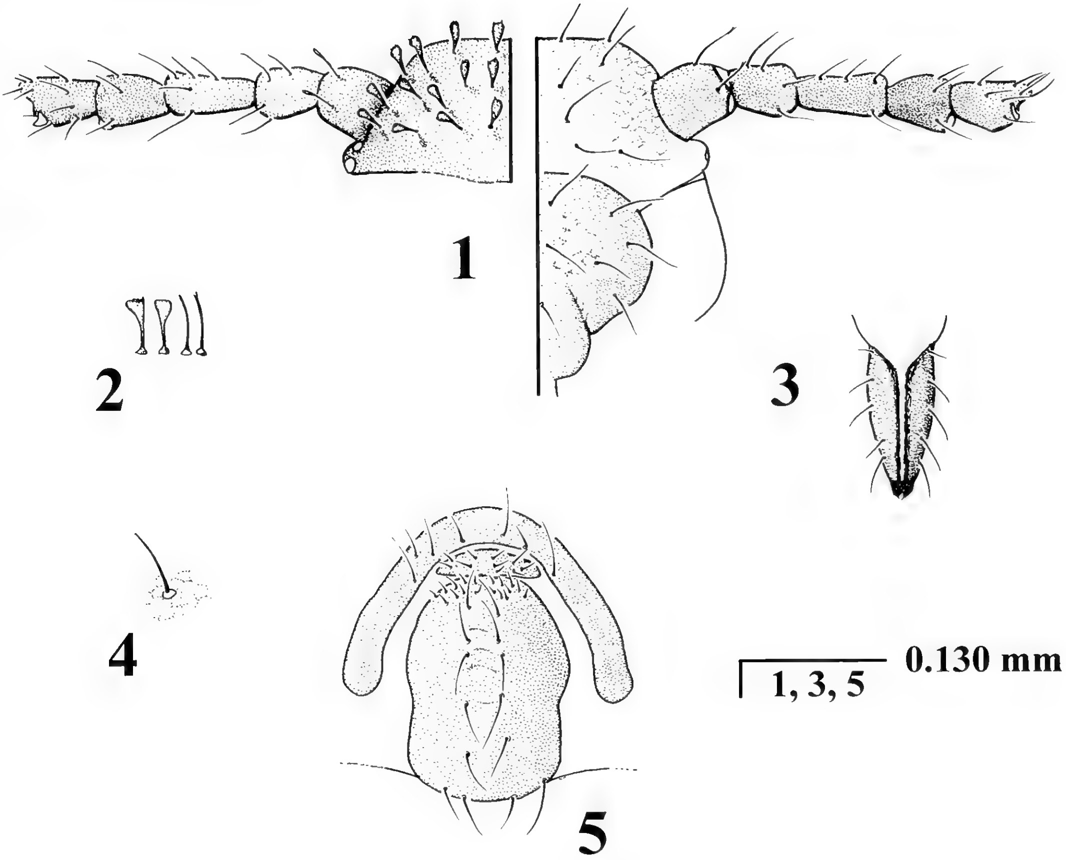
Key Words: Aphidoidea, North America, key, turfgrass

The genus *Geoica* (Hemiptera: Aphididae) is comprised of at least 14 species worldwide with the possibility of *Geoica utricularia* (Passerini) representing a complex of species (Eastop and Hille Ris Lambers 1976, Remaudière and Remaudière 1997). *Geoica* is considered an Old World genus (Blackman and Eastop 2000) and, until recently, four species of *Geoica* were recognized from North America: *Geoica lucifuga* (Zehntner), *Geoica pellucida* (Buckton), *Geoica squamosa* Hart, and *Geoica utricularia* (Passerini) (Smith and Parron 1978). However, *Geoica pellucida* (Buckton) and *Geoica squamosa* Hart are now both considered synonyms of *Geoica utricularia* (Passerini) (Remaudière and Remaudière 1997). Certain members of this genus exhibit a complex, 2-year life cycle with alternation between galls on *Pistacia*, pistachio (Anacardiaceae), and migration to and from their secondary host where populations feed on the roots of Gramineae and occasionally Cyperaceae (Brown and Blackman 1994, Blackman and Eastop 2000).

Geoica setulosa (Passerini) has been recorded from northwestern and central Europe, Italy, Iran, Turkey, and has recently been reported as occurring in the United States from Idaho (Blackman and Eastop 2000). Recent collections of *G. setulosa* from Kentucky indicate that it has a much greater distribution than its first collection from Idaho would indicate. In Iran, *G. setulosa* is holocyclic with its primary host, *Pistacia khinjuk* Stocks. In Europe, it is exclusively anholocyclic on grass roots (Blackman and Eastop 2000). Collections of *G. setulosa* in the United States have been made from roots of grasses and English plantain.

MATERIALS AND METHODS

Synoptic descriptions are based on published descriptions as well as material from the Aphididae portion of the National Collection of Insects (USNM), Beltsville, Maryland. In Specimens Examined, apterous adults are abbreviated as "ap. ad." For specimens collected at the same locality, on the same date, and from the same host plant as previously listed, the duplicate information is not repeated. Unless otherwise not-



Figs. 1–5. *Geoica setulosa*. 1, Dorsal (left) and ventral (right) aspects apterous adult female head and antennae. 2, Variations of body setae. 3, Ultimate rostral segment. 4, Acuminate ventral abdominal seta with polygonal reticulate pattern. 5, Anal plate region.

ed, voucher material consists of a single slide (sl.). Specimens were measured using a Nikon Eclipse E600™ compound microscope. Measurements are presented in millimeters (mm) as minimum and maximum ranges of representative specimens.

Geoica setulosa (Passerini)
(Figs. 1–5)

Tychea setulosa Passerini 1860: 40.
Tycheoides setulosa: Theobald 1916: 52.
Geoica setulosa: Theobald 1929: 197.
Geoica herculana Mordvilko 1935: 215.
Geoica setulosa: Eastop and Hille Ris Lambers 1976: 204.
Geoica setulosa: Heie 1980: 198.
Geoica setulosa: Remaudière and Remaudière 1997: 240.

Field characters.—Coloration of apterous viviparous females range from "... dirty whitish or greenish grey ..." (Heie 1980) to "... yellowish-white to greyish-white, some creamy ..." (Theobald 1929); "... antennae dusky, apices darkened; legs brown; rostrum dark at apex ..." (Theobald 1929). In specimens preserved in EtOH the head, prothorax, legs, antennae, and rostrum are crineous, the last segment of the rostrum is fuscous, and the base of most body setae is delineated by slight amber markings. Body form is globose.

Recognition characters from slide-mounted specimens.—Apterous viviparous female (Figs. 1–5): Body ovoid without wax gland plates, length 1.500–2.136 mm; width through eyes, 0.279–0.409 mm. Eye with three ommatidia. Antenna 5-segmented (Fig. 1), shorter than body, slightly darker than rest of body, without secondary sensoria, primary sensoria elongate and everted; length of segment: I, 0.062–0.086 mm; II, 0.062–0.081 mm; III, 0.093–0.123 mm; IV, 0.062–0.068 mm; base of V, 0.056–0.074 mm; terminal process of V, 0.019–0.031 mm. Setae on body and appendages variable, ranging from acuminate, multifid, capitate, to flabellate (Fig. 2), with dense random placement on dorsum. Rostrum extending to metacoxae; length of ultimate segment (Fig. 3), 0.136–0.167 mm, with 8–10 accessory setae, shorter than hind tarsal segment II. Length of metafemur, 0.223–0.279 mm; metatibia, 0.217–0.310 mm; metatarsus II, 0.087–0.093 mm. Abdominal venter with polygonal reticulate pattern (Fig. 4). Cornicles absent. Anus positioned dorsally, anal plate rectangular with numerous small setae dorsally and a median row of paired setae (Fig. 5).

Biology.—*Geoica setulosa* is anholocyclic in Northern and Central Europe with alatae being extremely rare or absent (Heie 1980). It feeds on the roots of grass species such as *Agrostis, Alopecurus, Corynephorus, Festuca,* and *Holcus* (Heie 1980) and has also been recorded from *Setaria* sp., *Oryza sativa* L., and *Triticum vulgare* Vill. [= *Triticum aestivum* L.] (Theobald 1929). It was reported in Idaho (Blackman and Eastop 2000) where it was collected on *Panicum capillare* L., *Poa pratensis* L., *Hordeum jubatum* L., *Echinochloa crus-galli* (L.) Beauvois, *Phalaris arundinaceae* L., *Avena fatua* L., *Setaria lutescens* (Weigel) F. T. Hubbard [= *Pennisetum glaucum* (L.) R.Br.], and "?crabgrass" (Halbert, personal communication). *Geoica setulosa* has also been associated with ants including *Lasius niger* (L.) (Theobald 1929) and *Lasius flavus* (F.) (Heie 1980, Blackman and Eastop 2000). *Geoica setulosa* collected in Kentucky always were found associated with the ant *Lasius neoniger* Emery on the roots of grass. Alatoid nymphs were collected in the population of *G. setulosa* and, while they could not be identified with certainty to species, we can assume that winged adults of *G. setulosa* may occur in Kentucky. *Geoica setulosa* is probably also anholocyclic in the United States.

Specimens examined.—U.S.A.: Kentucky, Lexington, University of Kentucky lawn #1, on Kentucky bluegrass [*Poa pratensis*], R. López collector, USNM: V-4-1999 (20 ap. ad. ♀ on 6 sl.); Spindletop Research Farm, on Kentucky bluegrass [*Poa pratensis*], R. López collector, USNM: V-24-1999 (1 ap. ad. ♀); Spindletop Research Farm, on Falcon II tall fescue [*Festuca arundinarea* Schreber], R. López collector, USNM: VI-19-1999 (16 ap. ad. ♀ on 6 sl.); on Aurora hard fescue [*Festuca longifolia* Thuill], R. López collector, USNM: VI-19-1999 (14 ap. ad. ♀ on 5 sl.); on Adelphi Kentucky bluegrass [*Poa pratensis* L. *adelphi*], R. López collector, USNM: VI-19-1999 (1 ap. ad. ♀); on Palmer II perennial ryegrass [*Lolium perenne* L.], R. López collector, USNM: VI-19-1999 (4 ap. ad. ♀ on 3 sl.); on Kentucky bluegrass [*Poa pratensis*], L., R. López collector, USNM: VI-25-1999 (1 ap. ad. ♀); on KY 31 tall fescue w/endophyte, R. López collector, USNM: VII-02-1999 (2 ap. ad. ♀).

KEY TO APTERAE OF NORTH AMERICAN *GEOICA*
(Modified from Blackman and Eastop 2000)

1. Anal plate with numerous subequal setae randomly dispersed . . . . . *Geoica utricularia* group
– Anal plate with median row of paired, long setae in addition to shorter dorsal setae (Fig. 5) 2
2. Dorsal body setae randomly placed; primary sensorium elongate; last rostral segment 0.136–0.167 mm long . . . . *Geoica setulosa* (Passerini)
– Dorsal body setae forming transverse rows; primary sensorium subcircular; last rostral segment 0.170–0.240 mm long . . . . *Geoica lucifuga* (Zehntner)

DISCUSSION

Although members of *Geoica* are not considered economically important (Foottit and Richards 1993), their association with grass and aphid-tending ants can be problematic. This is especially true where closely-mowed turfgrass is managed on golf courses. Associated ants, e.g., *L. neoniger*, tend to build mounds around the plants that serve as hosts for *Geoica*. These ant mounds are not only unsightly but they smother the grass, dull mower blades, and disrupt the smoothness and uniformity of playing surfaces, including tees, fairways, and putting greens (López and Potter 2000).

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COMPARATIVE ECOLOGY OF THE GENUS *LECONTELLA* WOLCOTT AND CHAPIN (COLEOPTERA: CLERIDAE: TILLINAE), WITH NOTES ON CHEMICALLY DEFENDED SPECIES OF THE BEETLE FAMILY CLERIDAE

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Abstract.—The genus *Lecontella* Wolcott and Chapin currently contains two species, *L. brunnea* (Spinola) from eastern North America and *L. gnara* Wolcott from southwestern North America. The results of the author's laboratory and field studies of *L. gnara* Wolcott are summarized, and this species' biology compared to that of *L. brunnea.* Larvae of *L. brunnea* are parasites in nests of solitary bees and wasps (Hymenoptera: Eumenidae, Sphecidae, and Megachilidae); adults have been collected at lights at night. The larva of *L. gnara,* which preys on immature stages of Cerambycidae and Buprestidae (Coleoptera), was described and illustrated by earlier workers under the name *Cymatodera morosa.* Adults of *L. gnara* are commonly collected at lights at night and have been reared from *Quercus arizonica* Sargent, *Prosopis* sp., and *Juglans* sp. Adult feeding, antennal grooming, and copulatory behaviors are described for *L. gnara,* and the presence of a chemical defense in adults of this species is noted for the first time.

Key Words: Cleridae, *Lecontella,* chemical defense, ecology, larvae, behavior

The genus *Lecontella* Wolcott and Chapin (1918) currently contains two species, *L. brunnea* (Spinola) and *L. gnara* Wolcott, both of which are large, nondescript, brown tilline clerids. *Lecontella brunnea* is widely distributed throughout eastern North America, while *L. gnara* is found in deserts of the southwestern United States and México. Despite the small size of this genus, its taxonomic history is quite complex, and for those interested in the details a review was provided by Ekis (1975). The taxonomy of *Lecontella* and its relatives is actively being studied by W. F. Barr (in litt.), and additions to this genus are expected in the near future.

In contrast to the wealth of taxonomic writings on the genus *Lecontella,* little has been published on the ecology of its species. The present paper includes substantial new information on the ecology of both species currently classified in *Lecontella.*

SEPARATING SPECIES OF *LECONTELLA*

The two species currently placed in *Lecontella* can be readily separated from species in most genera of Tillinae by the elongate, slender form of the terminal antennomere and the presence of rows of large elytral punctures that continue until the elytral apices. The sympatric genus with which *Lecontella* shows greatest affinity (and with which its species are most often confused in collections) is *Cymatodera* Gray, a large New World genus that has been the subject of considerable careful study by W. F. Barr for the past fifty years. The combination of antennal form and elytral punctures will separate *L. gnara* and *L. brunnea* from sympatric species of *Cymatodera.*

Characters for separating the two currently recognized species of *Lecontella* were discussed by Wolcott (1927). Of the characters listed by Wolcott, I have found the relative size of the pronotal punctures (large and dense in *L. gnara,* small and sparser in *L. brunnea*) to be the most reliable feature for separating adult specimens of these two species. Further information on the identification and relationships of *Lecontella* species will be provided by W. F. Barr in a forthcoming paper.

ECOLOGY OF *LECONTELLA BRUNNEA* (SPINOLA)

References.—Rau (1944); Bitner (1972); Foster and Barr (1972).

Larva.—Larvae of *L. brunnea* are parasites in the nests of solitary bees and wasps in the families Eumenidae, Megachilidae, and Sphecidae. Bitner (1972) found larvae of *L. brunnea* in nests of the following species of Hymenoptera in Indiana, USA: Eumenidae: *Monobia quadridens* (L.); Megachilidae: *Megachile* sp., *Osmia coerulescens* (L.), *Osmia lignaria* Say; Sphecidae: *Isodontia auripes* (Fernald), *Trypargilum clavatum* (Say), *Trypargilum striatum* (Provancher).

Adult habits.—Labels accompanying adult specimens of *L. brunnea* in NMNH indicate that adults are most frequently collected at lights at night. Adults also have either been reared from or found dead in the nests of bees and wasps. Rau (1944) reported finding adults of this species in the cells of nests of the mud-dauber wasp *Sceliphron caementarium* (Drury) (Hymenoptera: Sphecidae). Foster and Barr (1972) noted that R. M. Bitner successfully reared adults of *L. brunnea* from nests of *Osmia lignaria, O. coerulescens, Megachile rotundata* (F.), *Monobia quadridens,* and *Trypargilum striatum.* Adult specimens in NMNH were reared from an abandoned *Polistes* nest (Hymenoptera: Vespidae), nest of *Megachile rotundata,* nest of *Trypoxylon striatum,* and a "mud dauber nest." The rearing record from an abandoned *Polistes* nest probably indicates parasitism of a megachilid bee species, as megachilids commonly reuse cells of abandoned *Polistes* nests.

ECOLOGY OF *LECONTELLA GNARA* WOLCOTT

References.—Böving and Champlain (1920) (as *Cymatodera morosa* LeConte).

Larva.—The mature larva of this species was described by Böving and Champlain (1921) under the name *Cymatodera morosa* LeConte. This larva was found in dead branches of *Quercus arizonica* Sargent infested by species of Cerambycidae and Buprestidae (Coleoptera); the adult reared from this larva (in NMNH) is unquestionably the species now known as *L. gnara* Wolcott. Rearing records in NMNH indicate that larvae of *L. gnara* are also found in *Prosopis* and *Juglans* spp. infested by buprestid and cerambycid beetles.

Adult habits.—This species is one of the most frequently encountered clerids at lights at night in deserts of southwestern North America. In my experience, adults of *L. gnara* are most abundant at lights on overcast, humid nights preceding summer "monsoon" thunderstorms. Adult specimens in NMNH were reared from *Quercus arizonica, Prosopis* sp., and *Juglans* sp.

Live material studied.—Eleven adult *L. gnara* collected at ultraviolet lights at night in Vail, Arizona, between 7 and 14 September, 1999, were kept alive for laboratory studies.

Adult feeding behavior.—Adults in captivity feed readily on small beetles of a wide range of families. Prey items are captured and manipulated using the first two pairs of legs. The mandibles are used to remove the legs of the prey, which are discarded. The mandibles then serve to nearly divide the prey's body in two at the junction of the prothorax and the mesothorax. Contents of the prothorax and head are consumed, and the prothorax and attached head is discarded. Contents of the mesothorax, metathorax, and abdomen are consumed last. Often the elytra and metathoracic wings are removed to reach the metathorax and abdomen. In Arizona, the bostrichid beetle *Dendrobiella aspera* (LeConte) (Coleoptera: Bostrichidae) was especially preferred, but beetles of the families Buprestidae, Cerambycidae, Dermestidae, Mordellidae, and Scraptiidae were also consumed. In the laboratory in New York, adults fed on small beetles of the families Buprestidae and Dermestidae, and also readily imbibed sweet syrupy liquids such as honey and maple syrup. Wolcott (1921) noted that species of the related genus *Cymatodera* were found on mesquite imbibing sap flowing from wounds. Given the fact that adults of *L. gnara* readily consumed sweet syrupy liquids in captivity, it is probable that adults of this species also feed on sap flowing from wounds on mesquite and other desert shrubs.

Antennal grooming behavior.—Adults clean their antennae in the same manner as species of *Cymatodera* (*C. bicolor* (Say), *C. hurdi* Barr, *C. inornata* (Say), *C. sobara* Barr, and *C. undulata* (Say)) studied by the author. Oral secretions are transferred to the ventral pads of one of the protarsi; that protarsus steps on the middle of the antenna on the same side of the body, pinning it to the substrate; and the head is moved in the opposite direction, pulling the antenna through. To clean the base of the antennae, the protarsus is rubbed along the basal half of the antenna beginning at the base of the scape.

Reproductive behavior.—Three male and female pairs of *L. gnara* were placed in separate containers. Repeated short (<1 minute) copulations were observed; as in most clerids, the male mounts the female from behind and the male's ventral surface is kept in proximity to the female's dorsal surface throughout copulation. Several likely oviposition substrates were presented to female *L. gnara* after copulation, including dead branches of *Prosopis* and *Quercus* spp. However, no oviposition was observed, and no first instar larvae were obtained, indicating that the conditions necessary for oviposition in this species were not met in the laboratory.

Chemical defense.—Adults of *L. gnara* emit a foul-smelling odor when handled. This odor was not emitted by adult beetles at rest and seems to be associated with disturbance. The odor is similar in smell to the defensive secretions of certain stink bugs (Hemiptera: Pentatomidae) and ladybird beetles (Coleoptera: Coccinellidae) from eastern North America, and undoubtedly could be used as a chemical defense against predation.

CHEMICAL DEFENSES IN CLERIDAE

The first report of a chemical defense in any species of Cleridae was provided by Marshall and Poulton (1902) in their classic study of the bionomics of South African mimetic insects. Marshall and Poulton (1902) reported that a bright orange clerid species (subsequently identified by Mawdsley (1994b) as *Aphelochroa fulva* Quedenfeldt, subfamily Clerinae) emitted a strong, "verbena-like" smell. Hawkeswood (1987) provided the second example of possible chemical defense in Cleridae, noting that Australian species of the genus *Eunatalis* (again, subfamily Clerinae) emitted strongly-smelling chemicals when handled. *Lecontella gnara* is the first clerid in the subfamily Tillinae identified as possessing a chemical defense, suggesting that chemical defenses may be more widespread in this family than previously thought.

The possible existence of chemical defenses against predation in adult beetles of the family Cleridae is of particular interest given the large numbers of clerid species that mimic venomous or chemically defended insects (Mawdsley 1994a). It is quite possible that many of these mimetic clerids are themselves chemically defended, and that the mimetic interactions in which these clerids participate are Müllerian, rather than Batesian.

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IMMATURE STAGES OF *MONTINA CONFUSA* (STÅL) (HETEROPTERA: REDUVIIDAE: HARPACTORINAE)

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Abstract.—The egg and five instars of the harpactorine *Montina confusa* (Stål) are described and illustrated. Descriptions include morphological and monphometric characters of specimens reared in the laboratory.

Key Words: Heteroptera, Reduviidae, Harpactorinae, *Montina confusa,* eggs, nymphs

The genus *Montina* Amyot and Serville is comprised of ten species (Maldonado Capriles 1990). Pais Bueno and Berti Filho (1984a, b) described the nymphs and adult male and female of *Montina confusa* Stål and gave notes on biological aspects. Freitas et al. (1991), Rosa et al. (1991), Consoli and Amaral Filho (1992) and Freitas (1995) evaluated prey consumption by this species reared under laboratory conditions.

In this paper, we redescribe the egg and five nymphal instars of *Montina confusa* because previous descriptions are inadequate and the morphological terminology does not follow that used for Reduviidae.

Materials and Methods

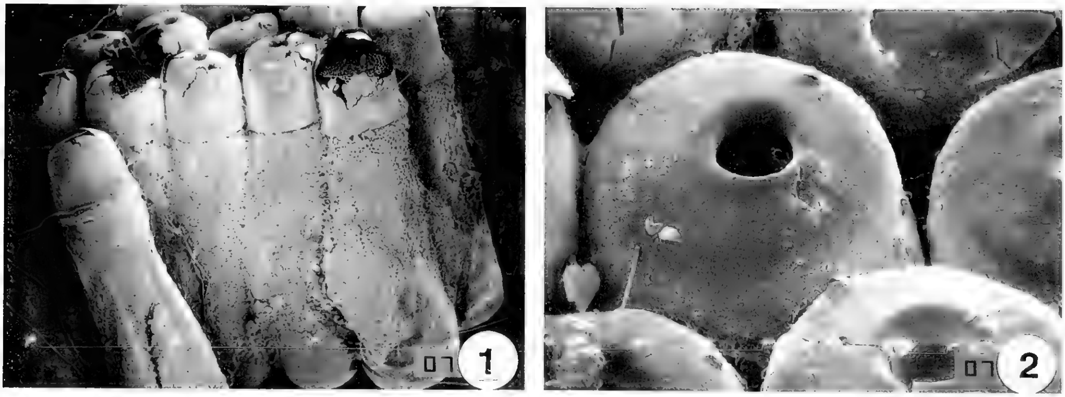
The material used in this study consists of eggs and specimens reared in the laboratory at the Instituto de Biologia, UNICAMP (Universidad do Campinas), Campinas, São Paulo, Brazil. The material was preserved in 75% ethanol. Terminology used for morphology follows that of Miller (1971) and Swadener and Yonke (1975). The measurements are given in millimeters (a total of 10 specimens for each instar). Illustrations were made with a drawing tube on a Wild M-stereomicroscope. Scanning electron micrographs of eggs and fifth instars were made from specimens mounted on stubs, sputter-coated with a gold palladium alloy, and studied with a JEOL T-100 SEM.

Description

Montina confusa Stål

Egg. (Figs. 1–2).—Length 2.23–2.34 (X = 2.29), diameter of operculum 0.386–0.466 (X = 0.416). Ova consist of regular masses of dark brown eggs cemented together by their margins. Egg cylindrical and elongated (Fig. 1). Chorion provided with well-developed perforations near apex. Most of chorion and entire surface of operculum covered with a mucilaginous substance. Operculum with a medial pore (Fig. 2).

First instar (Fig. 3).—Total length 3.00–3.40 (X = 3.22). Length of head 0.92–1.00 (X = 0.97), width of head 0.50–0.57 (X = 0.52). *Head:* Pyriform, yellowish, stained with dark brown behind eyes; setae short, longer posteriorly. Postocular region surrounded. Labrum and clypeus brown distally; clypeus and gena pilose. Eyes intense red, prominent, rounded anteriorly, truncate



Figs. 1–2. Micrographs of *Montina confusa* eggs. 1, General aspect in lateral view, 35×. 2, Chorion and operculum, 150×.

posteriorly, not passing superior or inferior edge of the head. Width of eye 0.07–0.10 (X = 0.08), interocular space 0.33–0.38 (X = 0.36). Rostrum yellow, segment I nearly glabrous, length 1.15–1.28 (X = 1.19), ratio of segment lengths ca. 1:1.41:0.48. Antenna elongate, filiform, segments I and IV pale brown, segments II and III dark brown, with finer and more abundant setae apically; length 4.32–4.94 (X = 4.71), ratio of segment lengths ca. 1:0.37:0.41:1.18.

Thorax: Pronotum pale brown, length 0.28–0.33 (X = 0.31), width 0.50–0.52 (X = 0.51), with two anterolateral tubercles; median sulcus with scattered setae. Propleuron pale brown; mesopleuron pale brown, dark brown ventrally; metapleuron dark brown, tinged with pale brown. Prosternum, mesosternum, and metasternun white, tinged with yellow. Wings pads absent. Legs yellowish, with irregular dark stains and scattered short setae.

Abdomen: Length 1.33–1.60 (X = 1.42), width 0.60–0.72 (X = 0.66); fusiform, pale brown; pilose.

Second instar (Fig. 4).—Total length 4.00–4.94 (X = 4.47). Length of head 1.38–1.55 (X = 1.49), width of head 0.67–0.73 (X = 0.71). *Head:* Pyriform, pale brown, similar to instar V; without spines or small stains in front of eye; ocelli outlined in red. Eyes similar to instar V. Width of eye 0.12–0.13 (X = 0.12), interocular space 0.45–0.48 (X = 0.46). Rostrum pale brown. Rostral length 1.63–1.78 (X = 1.68), ratio of segment lengths ca. 1:1.24:0.47. Antenna elongate, filiform, dark brown, segments III and IV yellowish; segment I with two whitish bands; all segments setose; lengths 6.62–7.09 (X = 6.86), ratio of segment lengths ca. 1:0.35:0.51:1.01.

Thorax: Pronotum dark brown, length 0.42–0.53 (X = 0.49), width 0.67–0.73 (X = 0.70), with two anterolateral tubercles. Median sulci present. Pleural area dark brown, tinged with pale brown, setose. Stridulatory sulci whitish. Prosternum, mesosternum, and metasternum pale brown. Area between wing pads pale brown. Wings pads 0.57–0.67 long (X = 0.60), dark brown. Legs yellowish to pale brown with irregular dark stains, tarsi darker brown; all segments setose; trochanter I densely pilose, black ventrally.

Abdomen: Length 1.15–1.33 (X = 1.26), width 0.70–1.25 (X = 1.06). fusiform, pale brown, with setae; scent glands on abdominal segments 3–5 pale brown; ventrally with black spots.

Third instar (Fig. 5).—Total length 5.70–6.33 (X = 6.00). Length of head 1.58–2.05 (X = 1.87), width of head 0.92–1.02 (X = 0.95). *Head:* Pyriform, pale brown, similar to instar V without spines; ocelli outlined in red. Eyes similar to instar V. Width of eye 0.15–0.22 (X = 0.18), interocular space

0.52–0.63 (X = 0.59). Rostrum similar to instar V, paler, especially first segment. Rostral length 2.19–2.42 (X = 2.32), ratio of segment lengths ca. 1:1.24:0.42. Antenna similar to instar V, with whitish bands on segment II and III. Antennal length 8.84–9.71 (X = 9.36), ratio of segment lengths ca. 1:0.36:0.63:0.87.

Thorax: Pronotum similar to instar V. Length of pronotum 0.67–0.77 (X = 0.73), width of pronotum 0.93–1.05 (X = 0.97). Pleural areas pilose. Stridulatory sulci whitish. Propleuron and mesopleuron pale brown tinged with orange except for dark margins on propleuron, posterior and inferior fringe dark on mesopleuron, metapleuron dark brown, pale brown medially. Prosternum, mesosternum, and metasternum whitish, tinged with pale brown. Area between wing pads pale brown, tinged with orange, whitish anterior and posteriorly. Wings pads 0.80–0.93 long (X = 0.86), dark brown, tinged with pale brown. Legs whitish, except coxae and femora pale brown distally. Coxae, trochanters, femora, and tibiae stained with dark brown. Trochanter I, femora I basally, and tibia I distally with dense black setae ventrally.

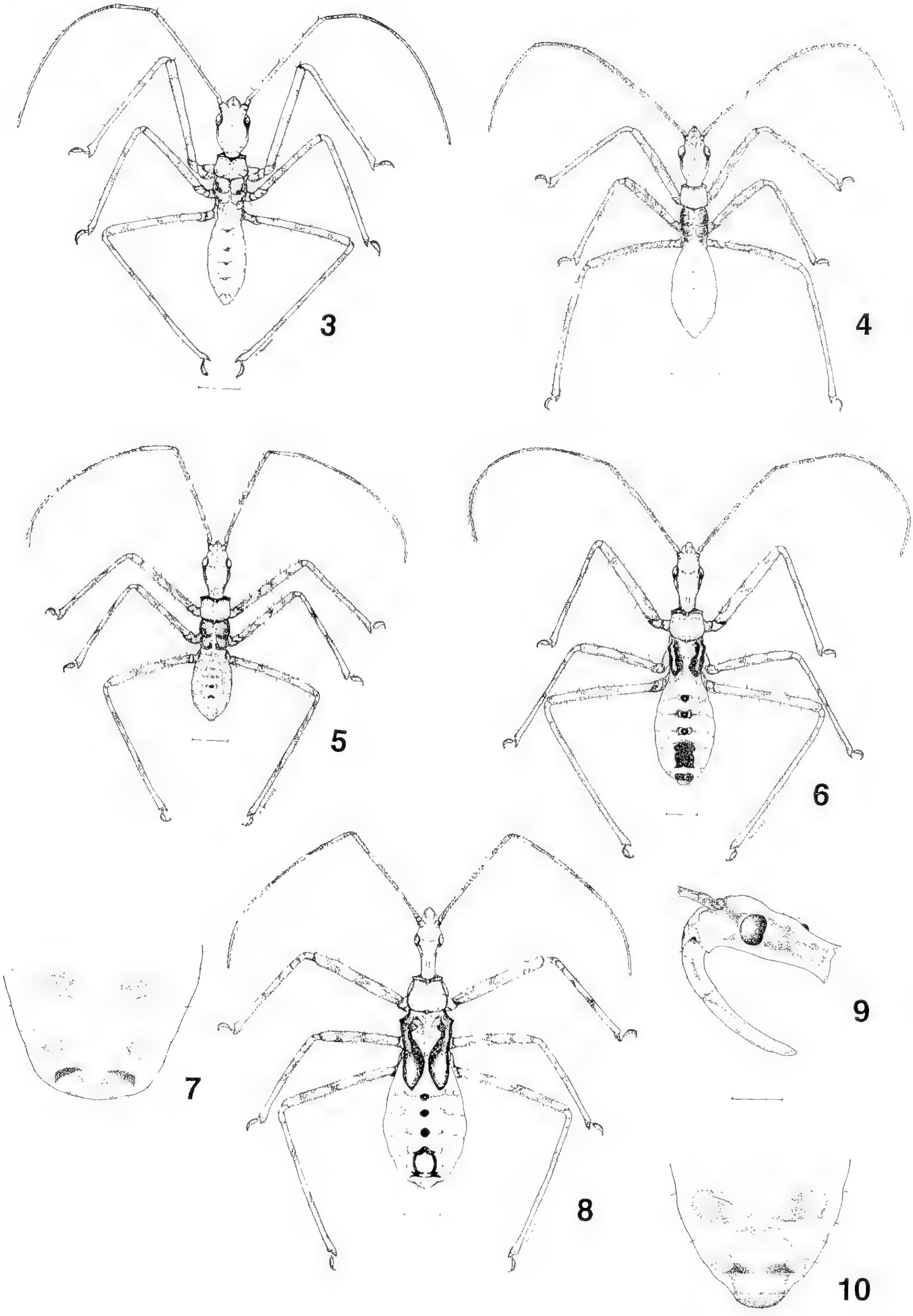
Abdomen: Length 3.00–4.00 (X = 3.48), abdominal width 0.95–1.42 (X = 1.21). Abdomen fusiform, pale brown, tinged with orange and whitish; setose; scent glands well developed on abdominal segments 3–5. Segment 1 whitish; segment 2 pale brown tinged with white; segment 3 dark brown tinged with white; segment 6 dark brown, with a black spot expanded laterally. Yellowish ventrally, tinged with pale brown; segments 4-6 red and white stained, with small black spots medially; segment 8 brown stained.

Fourth instar (Fig. 6).—Total length 8.10–9.12 (X = 8.37). Length of head 2.63–2.93 (X = 2.79), width of head 1.17–1.30 (X = 1.21). *Head:* Similar to instar V, with spines; ocelli less distinctly outlined in red, in some specimens superior border of gena dark. Eyes as instar V. Width of eye 0.20–0.27 (X = 0.23), interocular space 0.68–0.83 (X = 0.75). Rostrum similar to instar V, segment I paler and stains on edges of III absent. Rostral length 2.83–3.47 (X = 3.12), ratio of segment lengths ca. 1:1.14:0.36. Antenna as instar V; length 11.89–13.08 (X = 12.35), ratio of segment lengths ca. 1:0.38:0.81:0.82.

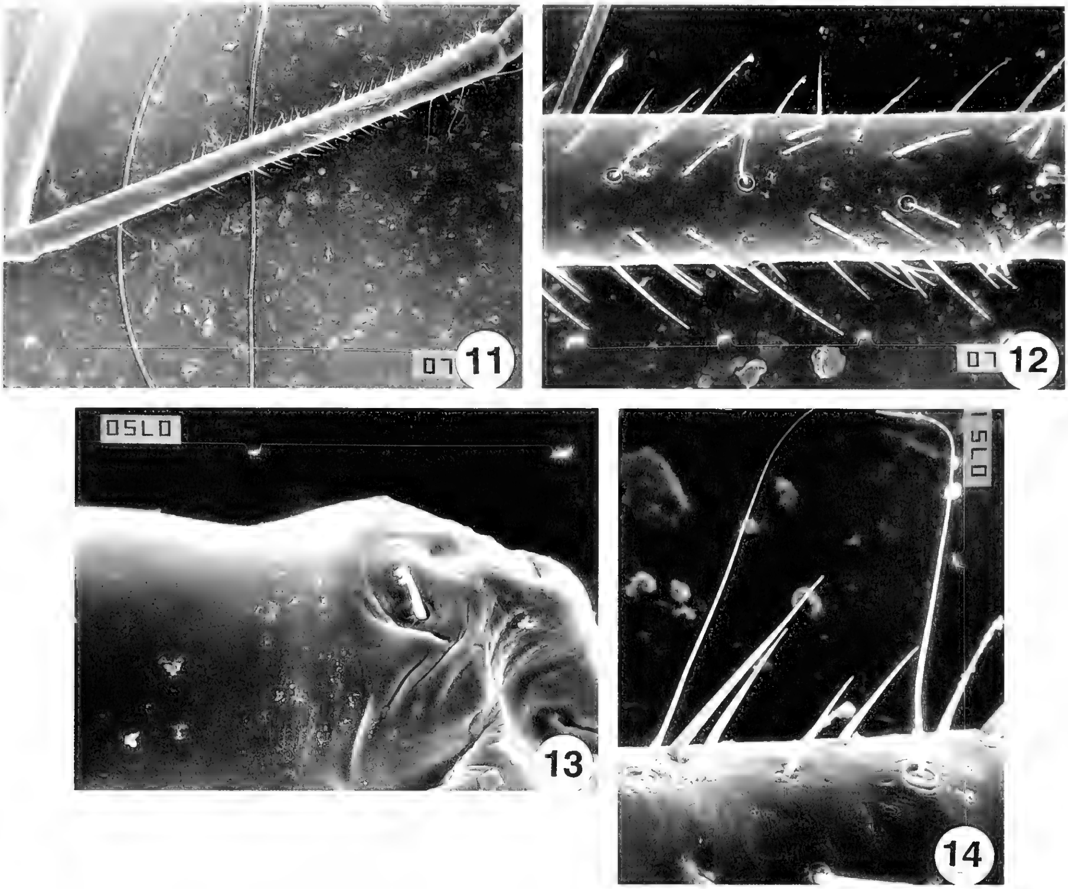
Thorax: Pronotum as for instar V. Length of pronotum 0.97–1.17 (X = 1.06), width of pronotum 1.30–1.55 (X = 1.41). Pleural areas pilose. Stridulatory sulci whitish. Propleuron and mesopleuron pale brown, tinged with orange, edges of propleuron dark brown, posterior and inferior fringe of mesopleuron and metapleuron dark brown, except medially pale brown. Prosternum, mesosternum and metasternum whitish, tinged with pale brown. Posterior lobe of pronotum pale brown, tinged with orange, posterior process whitish, with two brown spots laterally. Wing pads 1.38–1.75 long (X = 1.58). Legs whitish or pale brown, except coxae, femora distally, and tibiae basally pale brown, tinged with red. Dark stains more distinct in instar V; all segments setose. Trochanter I, femur I, and tibia I densely pilose, black ventrally.

Abdomen: Length 4.18–4.68 (X = 4.36), width 1.67–2.43 (X = 2.06). Abdomen fusiform, pale brown, tinged with orange; setose; segments 1 and 2 with whitish stains medially; scent glands well developed. Segment 6 with a black spot expanded laterally in same position as scent glands of anterior segments. Two whitish stains lateral to scent glands. Segments 4–6 with a red fringe distally and whitish stains centrally, in some specimens. Connexivum whitish distally and white continuing to the medial part of the abdomen. Segment 7 with a rectangular dark stain; segment 8 with a dark stain expanded laterally. Pale brown with lateral white lateral spots bordered in red. Ventrally pale brown (some specimens with black points), medially pale. Apical segments darker externally (Fig. 7).

Fifth instar (Fig. 8).—Total length 12.41–15.19 (X = 13.98). Length of head 3.47–4.07 (X = 3.70), width of head 1.50–



Figs. 3–10. *Montina confusa.* 3, First instar. 4, Second instar. 5, Third instar. 6, Fourth instar. 7, Fourth instar, ventral aspect of last segments of abdomen. 8–10, Fifth instar. 9, Head, lateral view. 10, ventral aspect of last segments of abdomen.



Figs. 11–14. *Montina confusa*, micrographs of antennal segment 2 trichobothria. 11, Antennal segment 2, 75×. 12, Medial trichobothrium, 350×. 13, Distal trichobothria, 750×. 14, Medial trichobothrium, 750×.

1.73 (X = 1.58). *Head:* Pyriform, pale brown, darker brown behind eyes, paler on neck, ocelli outlined in red; laterally (Fig. 9) with a stripe from antenna to eye, a small stain in front and an other stain posteriorly brown; labrum and clypeus dark brown, buccula distally dark brown. Eyes prominent, rounded anteriorly and truncated posteriorly, intense red, not passing superior or inferior edge of head. Width of eye 0.28–0.65 (X = 0.47), interocular space 0.90–1.10 (X = 0.99). Rostrum pale brown, stained dark brown (in some specimens joint of I and II darker); II and III paler than I and with more setae. Stain basally on I, II, and along edges on III. Rostral length 3.67–4.64 (X = 4.12), ratio of segment lengths ca. 1:1.12:0.40. Antenna elongate, filiform, dark brown to almost black, paler on III and IV; two whitish bands on segment I, one on segments II and III; setae finer, more abundant distally. Segment II with a trichobothrium as seen in Figs. 11–14. Antennal length 15.08–17.19 (X = 16.04), ratio of segment lengths ca. 1:0.38:0.92:0.71.

Thorax: Pronotum orange (tinged with red in some specimens), with two anterolateral tubercles and anterior margin dark brown; with setae. Median sulci present, with sparse, short setae. Length of pronotum 1.47–2.00 (X = 1.71), width of pronotum 1.85–2.53 (X = 2.17). Propleuron and mesopleuron pale brown, tinged with orange, except dark brown margins, with narrow, pale borders. Stigma whitish interiorly.

Metapleuron dark brown, except basally and medially pale brown. Pleura pilose. Prosternum dark brown except stridulatory sulci whitish. Mesosternum and metasternum whitish, tinged with pale brown, a central fringe of black setae on mesosternum in some specimens. Scutellum pale brown, tinged with orange, posterior process whitish. Wings pads 3.64–4.37 long (X = 3.93), pale yellow, dark brown basally and along edge. Legs pale brown, tinged with pale yellow; coxae, femora distally, and tibiae basally pale brown, tinged with red; tarsi brown. Trochanters, femora, and tibiae tinged with dark brown. Trochanter I, femur I, and tibia I densely setose, black ventrally.

Abdomen: Length 6.52–7.91 (X = 7.28), abdominal width 3.17–3.92 (X = 3.53). Abdomen fusiform, pale brown, tinged with orange; setose; scent gland well developed on abdominal segments 3–5, consisting of black papilas, except base of first papila pale brown. Segment 6 with a black spot expanded laterally in same position as scent glands of anterior segments. Two whitish stains lateral to scent glands. Segments 3–6 with a red fringe distally, surrounded by whitish stains centrally. Connexivum distally and continuing to the medial part of the abdomen whitish; the remainder brown, tinged with orange. Pale brown ventrally, tinged with red surrounded by whitish spots laterally, last segments darker externally (Fig. 10).

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A REVIEW OF THE SIRICID WOODWASPS AND THEIR IBALIID PARASITOIDS (HYMENOPTERA: SIRICIDAE, IBALIIDAE) IN THE EASTERN UNITED STATES, WITH EMPHASIS ON THE MID-ATLANTIC REGION

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Abstract.—Keys are presented for the five genera and 15 species of adult Siricidae and one genus and two species of their parasitoids of the family Ibaliidae that occur in or may be adventive in eastern United States. Siricid larvae are wood borers in conifers and broadleafed trees. Notes on their biology, fungal symbionts, distributions and host associations are given. Data from collections in the mid-Atlantic states include seasonal occurrence of both Siricidae and Ibaliidae.

Key Words: *Sirex, Urocerus, Tremex, Xerix, Eriotremex, Ibalia,* fungal symbionts

Worldwide, there are 85–100 species of Siricidae in two subfamilies and 11 genera (Smith 1978, 1993). The subfamily Tremicinae is associated with angiosperms and Siricinae with gymnosperms. The family is widespread in the deciduous and coniferous forests of the northern hemisphere, extending south to Cuba, northern Central America, New Guinea, Philippines, Viet Nam, northern India, and northern Africa; one genus with two species is Afrotropical. No Siricidae are native to Australia and South America.

All species for which larvae are known bore into weakened or dying trees (Middlekauff 1960, Smith 1979). Most species in their native range are considered to be of minor importance except for decreasing the value of lumber; however, introduced, exotic species can be very damaging. Because larvae of siricids feed and develop in wood, with several years required for their life cycle, they are commonly transported in lumber by commerce. Thus, non-native species may emerge in buildings constructed of lumber that originated in other parts of the country or from other nations. For example, *Sirex noctilio* (F.) is a European species that became a major pest of *Pinus radiata,* an American species, when *P. radiata* was planted in New Zealand and Australia (Gilbert and Miller 1952, Rawlings 1955, Gaut 1970). A major control effort in the 1960's and 1970's used parasitic nematodes to control *S. noctilio* (Bedding and Akhurst 1974). *Sirex noctilio* is now considered to be the most important threat to new *P. radiata* plantations in South Africa, Brazil, and Argentina (Stival et al. 1993; Iede et al. 1998; Tribe 1995, 1997). In the early 1970's, an Asian species, *Eriotremex formosanus* (Matsumura), was accidentally introduced into the southeastern United States where it has spread rapidly (Smith 1975, 1996). It attacks hardwoods, including oaks, but it is not considered to be a major pest at this time. More recently, a Palearctic species, *Urocerus sah* (Mocsáry), was reported in New Hampshire (Smith 1987).

The Ibaliidae (Cynipoidea) are part of the parasitoid complex of Siricidae. We include them here because we recorded their presence in collections from the mid-Atlantic states and are able to present their seasonality in relation to that of their hosts.

Keys for the identification of the eastern United States species of Siricidae have been non-existent since Bradley's (1913) revision, although Smith (1987) published a key to North American *Urocerus,* and Stange (1996) gave a key to the six species of Siricidae in Florida. Johnson (1928) gave some notes on New England species and illustrated them, but he did not give a key to species. For the Ibaliidae, Liu and Nordlander (1992, 1994) published a revision of world and North American Ibaliidae. Here, we give keys for identification of the eastern U.S. Siricidae and Ibaliidae, summarize their distribution and hosts, and present seasonal activity of some species with emphasis on collections from the mid-Atlantic states.

General biology

Like other wood-boring insects, siricids do not make the enzymes that digest cellulose, the major energy source for wood feeders (Kukor and Martin 1983). To utilize cellulose, wood-boring insects live in symbiotic relationships with other organisms that produce cellulases (Buchner 1965, Francke-Grosmann 1939). Siricids use basidiomycetous wood-decay fungi to break down cellulose (Buchner 1928; Cartwright 1929, 1938). The relationship between siricids and these fungi is true symbiosis, as organisms derive benefit. The siricids gain the ability to utilize a large energy source, cellulose, and the fungus benefits because it is not only carried to a specific host tree, but it is also injected underneath the bark, past the tree's first line of defense. Female siricids, except in the genus *Xeris,* carry oidia (hyphal fragments) of the fungus in specialized, abdominal glands called mycangia that have ducts leading to the reproductive tract (Buchner 1928). When the wasp lays her eggs, oidia are also deposited. The fungus grows rapidly and secretes digestive enzymes onto the substrate. When the larvae hatch, they commence feeding on the fungus and digested wood. There is some disagreement about whether or not the insects actually consume the wood or feed on the fungi alone (Gilbertson 1984). In either case, however, wood is the ultimate source of energy for the larvae. Exactly how adult females acquire the fungus after the larvae pupate is also uncertain (Gilbertson 1984), but female larvae have specialized hypopleural organs (Parkin 1941, 1942; Stillwell 1965) that may play a role in scraping fungus from the tunnel walls which is then somehow incorporated into the mycangia.

Larvae take from one to three or more years to reach pupation and emerge as adults (Middlekauff 1960, Stillwell 1967, Smith 1993). Males are commonly reared but seldom seen in the field. They are occasionally seen in small groups at the tops of trees (Middlekauff 1960; Schiff, personal observation). In the western United States, many species are attracted to forest fires, where females lay eggs into charred trees. Forest fires are much less common in the eastern United States, and there are no data on eastern siricid species being attracted to fires in this region. Species of the genus *Xeris* do not appear to carry a wood decay fungus in mycangial glands; instead, they limit oviposition to substrates that have already been inoculated with a wood decay fungus by another species of siricid (Francke-Grosmann 1939, Fukuda and Hijii 1997).

FUNGI

The identity of the fungal symbionts used by siricids has been complicated by both the difficulty in inducing the fungi to produce fruiting bodies in vitro and in some cases by misidentifications of the siricids involved (Gilbertson 1984, Gaut 1970). The fungal symbionts of only two tremicine species have been identified: *Tremex columba* (L.) from North America and *Tremex longicollis* Konow from Japan, both of which harbor *Cerrena* (*Daedalea*) *unicolor* Bull. ex Fries (Stillwell 1964, Tabata and Abe 1995). The siricines use fungi in the genus *Amylostereum,* and there are three species worldwide: *A. chailettii* (Pers.: Fr.) and *A. laevigatum* (Fr.) that occur in the United States, and *A. areolatum* (Fr.) that is not known from the United States (Farr et al. 1995). All United States siricines whose symbionts have been determined (*Sirex cyaneus, S. nigricornis, S. edwardsii, S. longicauda, S. juvencus californicus, Urocerus albiconris, U. gigas flavicornis,* and *U. californicus*) use *A. chailettii* (see Gilbertson 1984 review). American isolates of fungus from *Sirex juvencus* have not been determined, but European examples use *A. areolatum* (Gaut 1970). If each siricid is faithful to a specific symbiont (Gaut 1970), then *Sirex juvencus* in America must use *A. areolatum,* and the fungus has simply not been found in the field as yet, or, the American *Sirex juvencus* is not the same as the European species. *Amylostereum areolatum* should also have been introduced with *Sirex noctilio,* its wasp symbiont, in places where that species was accidentally introduced.

MALAISE TRAPPING AND VIRGINIA SPECIES

This study is supplemented by material collected in Virginia and adjacent states over the past 18 years and specimens in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and Virginia Polytechnic Institute and State University, Blacksburg, Virginia (VPI).

Collections were made using Malaise traps which were set up and in continual use in different localities from approximately March through the first of November. Siricidae and Ibaliidae are not commonly collected this way, but enough have accumulated over the years of collecting to help verify what occurs in this region and indicate the seasonal activity of some species. Totals collected are 163 specimens of 5 species of Siricidae and 149 specimens of 2 species of Ibaliidae. The Siricidae are represented mainly by 133 specimens of *Tremex columba* (L.), associated with broad-leaved trees, and 126 specimens of its parasitoid, *Ibalia anceps* Say. The other Siricidae, 30 specimens of the genera *Urocerus* and *Sirex,* are associated with conifers, and 23 specimens of their parasitoid *Ibalia leucospoides* (Hockworth). All Siricidae collected in Malaise traps were females.

Seven species of Siricidae and two species of Ibaliidae occur in Virginia. We have been able to verify several exotic species, e.g., *Sirex longicauda* Middlekauff, but there are undoubtedly others. Another nonnative species is *Eriotremex formosanus* (Matsumura), an introduced species in southeastern U.S. which has been found in extreme southeastern Virginia.

MATERIALS AND METHODS

The keys are valid for eastern United States, east of the Rockies, and eastern Canada. Species not native to this region but are possible adventives in imported lumber are included. There are no confirmed collections of *Sirex noctilio* from eastern U.S., but it is included it in the key because the species has a history of introductions in other parts of the world and specimens are occasionally intercepted at ports-of-entry in the U.S.

Recorded distributions and host plants are from the literature and examined specimens. The following are given for each species: distribution (state/province from which recorded); Virginia records; collection records (from Malaise trapping in Maryland, Virginia, and West Virginia); hosts (as recorded); and remarks.

Records in the collections sections are cited only by county. Specific data are as

Fig. 1. *Sirex nigricornis* (arrow points to cornus).

follows: MARYLAND: Allegheny Co., Green Ridge State Park.; Prince George's Co., Beltsville Agricultural Research Center. VIRGINIA: Clarke Co., University of Virginia Experimental Farm and State Arboretum of Virginia, 2 mi S Boyce; Essex Co., 1 mi SE Dunnsville; Fairfax Co., near Annandale; Louisa Co., 4 mi S Cuckoo; Loudoun Co., nr. jct. of Sycolin Road and Goose Creek. WEST VIRGINIA: Hardy Co., 3 mi NE Mathias, 38°55′N, 78°49′W; Tucker Co., Fernow Experimental Forest, south of Parsons.

Literature references to original descriptions and synonymies are found in Smith (1978, 1979). Only significant or subsequent literature is presented here.

The use of pits on the lancet for species separation were first used by Viitasaari (1984) and Viitasaari and Midtgaard (1989). The size, form, and location of the lateral ridges and pits may be significant for species identification. They are used here mainly to separate *Sirex noctilio* from the native North American species of *Sirex*.

Males are more difficult to separate than females. Use caution in the keys to males since color variation may be more extensive than we have observed.

RESULTS

Siricidae

KEY TO GENERA OF NORTH AMERICAN SIRICIDAE

1. Hindtibia with two apical spurs; antenna with 18 or more segments, usually more than 22 2
– Hindtibia with one apical spur; antenna with more than 22 segments in *Xeris,* less than 22 segments in *Tremex* and *Eriotremex* 3
2. Head usually with large white spot behind each eye; female cornus long and slender, constricted at base (Fig. 2); male hindtarsus slender, first segment 4 or more times longer than broad, commonly 5–6 time longer, second and third segments 2 times or more longer than broad (Fig. 6) . . . . *Urocerus*
– Head black; female cornus short, triangular, not constricted at base (Figs. 1, 3, 4); male hindtarsus stout, laterally flattened, first segment 4 times or less longer than broad, second and third segments triangular, slightly longer or about as long as broad (Fig. 5) . . . . *Sirex*

Antenna with 15–21 segments; head without genal carina behind eyes; female ovipositor shorter than forewing; hindwing with anal cell 4

Antenna with 23 or more segments; head with a genal carina behind each eye (Figs. 7, 8); female ovipositor longer than forewing; hindwing without anal cell . . . . *Xeris*

4\. Antenna with 14–15 segments; body without long golden hairs . . . . *Tremex*

– Antenna with 20–21 segments; body with long golden hairs . . . . *Eriotremex*

Comments.—Use of the white spot behind each eye to separate *Urocerus* and *Sirex* is commonly used in keys but is not infallible. Although most specimens can be separated by this, a series of *Urocerus cressoni* from Virginia varies from an entirely black head to some with a distinct white spot. Examination of the shape of the female cornus and the male hind tarsus should be checked for determination. The more slender, more rounded hindtarsus (Fig. 6) of *Urocerus* vs. the stout, laterally flattened hindtarsus (Fig. 5) of *Sirex* males is a good character for the eastern species.

SUBFAMILY SIRICINAE

Genus *Sirex* Linnaeus

The most recent key is to the species of California by Cameron (1967). Two species, *S. edwardsii* and *S. nigricornis,* are widespread in eastern U.S. *Sirex cyaneus* is northern but extends south in the Appalachians to North Carolina, *S. juvencus* is northern and transcontinental, *S. behrensii* has only been recorded from Virginia and emerging from imported wood in Florida, and two species, *S. areolatus* and *S. longicauda,* are adventive in the eastern states emerging from wood.

KEY TO SPECIES

1\. Female 2

– Male 9

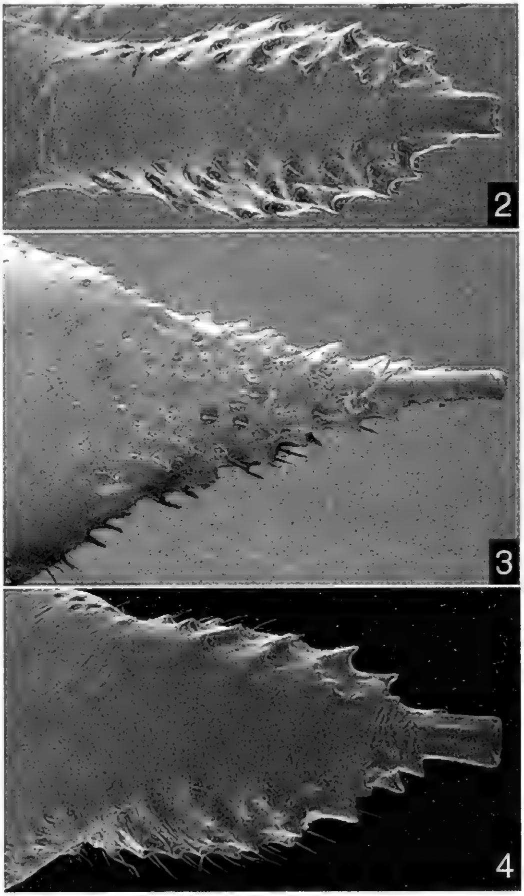
2\. Ovipositor longer than forewing 3

– Ovipositor shorter than forewing 4

3\. Tibiae and tarsi red . . . *longicauda* Middlekauff

– Legs entirely black or blue black . . . . *areolatus* (Cresson)

4\. Abdomen mostly red, but may be infuscated to black at base, laterally or ventrally 5



Figs. 2–4. Female cornus. 2, *Urocerus cressoni.* 3, *Sirex cyaneus.* 4, *Sirex longicauda.*

– Abdomen entirely black or blue black 6

5\. Legs black, only tarsi reddish brown; wings darkly, uniformly infuscated (Fig. 1) . . . . *nigricornis* (Fabricius)

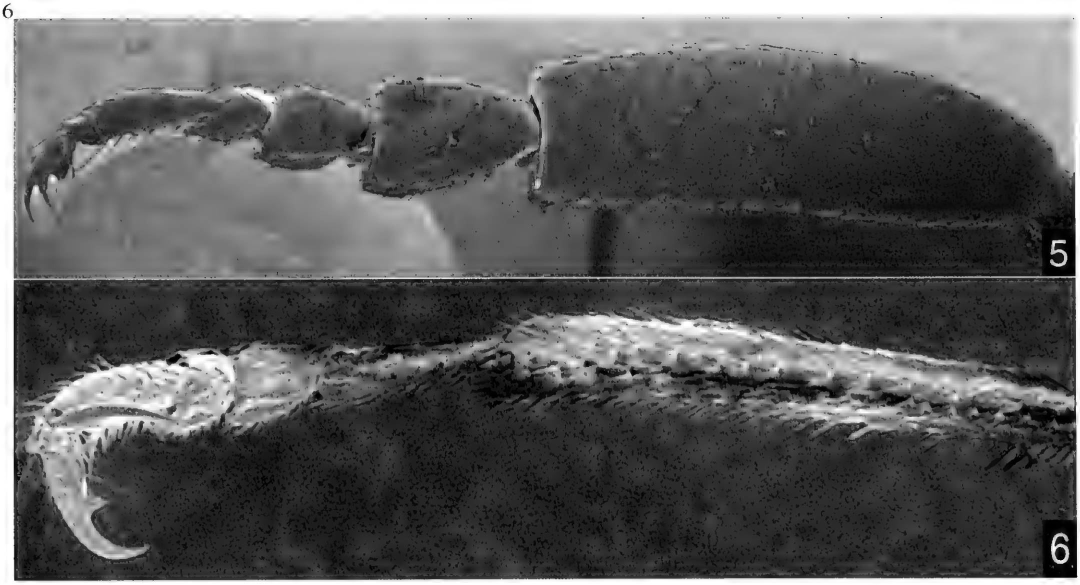
– Legs with tibia and tarsi reddish brown; wings hyaline, forewing with fuscous band below stigma and fuscous apical margin . . . . *behrensii* (Cresson)

6\. Legs black . . . . *edwardsii* Brullé

– Legs largely orange 7

7\. Apical tarsal segment black; sawsheath (valvula 3) shorter than oblong plate (valvula 2); length of ovipositor as long as distance from base of wing to base of radial cell; mesopleuron densely punctured, in the middle with interspaces mostly smaller than punctures (Fig. 9); pits of lancet large and close together (Fig. 11); antenna black . . . . *noctilio* (Fabricius)

– Tarsi yellow to orange; sawsheath (valvula 3) as long as or longer than oblong plate (valvula 2); length of ovipositor as long as distance



Figs. 5–6. Hindtarsus. 5, *Sirex edwardsii*. 6, *Urocerus cressoni*.

from base of wing to beyond base of radial cell; punctures at middle of mesopleuron farther apart, with shining flat interspaces mostly broader than punctures (Fig. 10); pits of lancet small and far apart (Fig. 12); antenna black or brown at base 8

8\. Sawsheath (valvula 3) longer than oblong plate (valvula 2); length of ovipositor as long as distance from base of wing to apex of radial cell; antenna black . . . *cyaneus* (Fabricius)

– Sawsheath (valvula 3) equal to oblong plate (valvula 2); length of ovipositor as long as distance from base of wing to middle of radial cell; basal segments of antenna often reddish brown . . . . *juvencus* (Linnaeus)

9\. Abdomen red, with only basal 1 or 2 segments black 10

– Abdomen black at both base and apex, black at apex may be only on dorsum or venter of apical segment 12

10\. Femora, tibiae and tarsi red; antenna pale at base; wings hyaline . . . . . . *behrensii* (Cresson)

– Hindleg black or black with femur red; midleg black; antenna black; wings yellowish 11

11\. Hindleg black, apical 2 tarsal segments yellowish . . . . *nigricornis* (Fabricius)

– Hindleg with femur red, tibia and tarsus black . . . . *cyaneus* (Fabricius)

12\. Legs entirely black (abdominal segments 2–7 orange; wings hyaline, stigma of forewing black) . . . . *areolatus* (Cresson)

– Legs partly reddish brown to orange 13

13\. Femora and rest of hindleg black 14

– Femora orange; apical 2–3 hindtarsal segments orange 15

14\. Abdominal segments 5 and 6 and sometimes part of 7 orange; wings yellow, stigma of forewing yellow . . . . *edwardsii* Brullé

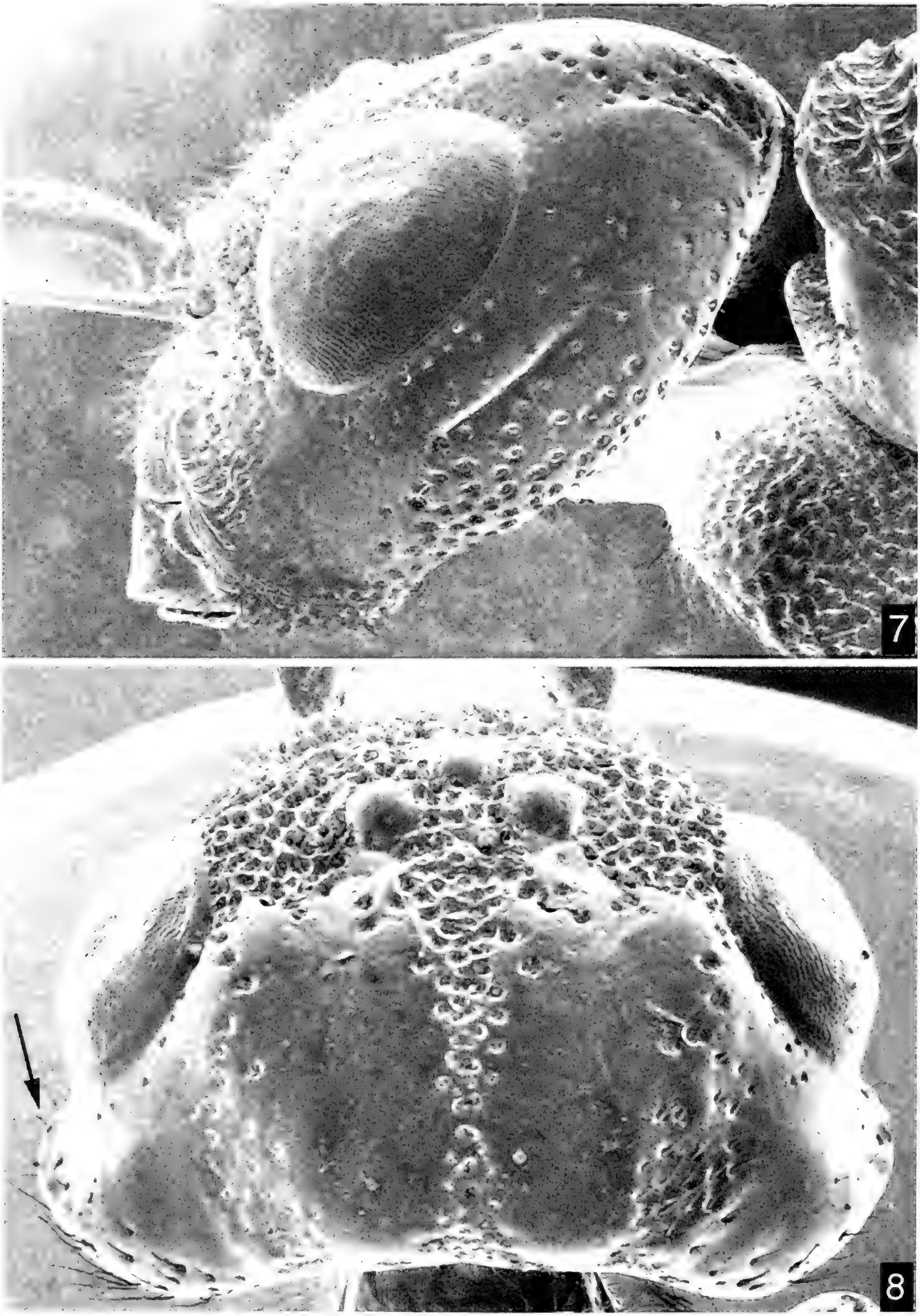
– Abdominal segments 3–7 and sometimes 8 orange; wings clear, hyaline, stigma of forewing black . . . . *longicauda* Middlekauff

15\. Basal antennal segments orange; apical tarsal segments yellow to orange; punctures of mesopleuron separated by flat, shining interspaces, usually broader than punctures (Fig. 10) . . . . *juvencus* (Linnaeus)

– Antenna black; apical two tarsal segments blackish; punctures of mesopleuron close together, interspaces usually shorter than punctures (Fig. 9) . . . . *noctilio* (Fabricius)

Sirex areolatus (Cresson)

Distribution.—Alabama, Arizona, Arkansas, British Columbia, California, Colorado, Florida, New Mexico, Oregon, Virginia, Washington (Middlekauff 1960, Smith 1979). The Florida specimens emerged from fir wood imported from western United States (Stange 1996). In Alabama, specimens were "found boring into sheet rock inside home," and in Arkansas, "ex sheet rock." It was found in Kauai, Hawaii "ex cedar wall."



Figs. 7–8. *Xeris spectrum.* 7, Head lateral view. 8, Head, dorsal view (arrows point to carina).

Virginia records.—Cape Henry, IX-13023, J.N. Knull, bald cypress (1 female, 2 males); Cape Henry, 9-9-24, W.S. Fisher (1 male).

Hosts.—*Cupressus macrocarpa, Juniperus occidentalis, J. scopulorum, Libocedrus decurrens, Pinus contorta, P. jeffreyi, P. lambertiana, P. radiata, Psuedotsuga menziesii, Sequoia sempervirens, Taxodium distichum, Thuja* sp. Commonly attacks redwood, cypress, and cedars; found less frequently on pines (Middlekauff 1960, Smith 1979).

Remarks.—The only eastern records known for this species are from Virginia and Florida. The Virginia collections appear authentic and are probably not from imported wood. Inasmuch as *S. areolatus* commonly attacks redwood, cypress, and cedars and is found less frequently on pines (Middlekauff 1960), this species could be established on baldcypress in the East. De Leon (1952) recorded it from *Sequoia sempervirens* in California, and Westcott (1971) from *Juniperus occidentalis* in Oregon.

Sirex behrensii (Cresson)

Distribution.—California, Idaho, Nevada, Oregon, Washington.

Hosts.—*Cupressus macrocarpa, Pinus jeffreyi, P. lambertiana, P. ponderosa, P. radiata,* Japanese pine (Middlekauff 1960, Smith 1979).

Remarks.—This species has been found in Ohio emerging from imported lumber: "Cleveland O., ex plaster wall."

Sirex cyaneus Fabricius
(Fig. 3)

Distribution.—Alabama, Alaska, Alberta, British Columbia, California, Colorado, Georgia, Idaho, Illinois, Kansas, Maine, Michigan, Minnesota, Montana, Nebraska, New Brunswick, New Hampshire, New Jersey, Newfoundland (Labrador), Nevada, New Mexico, New York, North Carolina, Nova Scotia, Oregon, Quebec, Utah, Washington, West Virginia, Wyoming (Middlekauff 1960, Smith 1979).

Hosts.—*Abies balsamea, A. concolor, A. fraseri, A. grandis, A. lasiocarpa, A. magnifica, Larix laricina; Picea engelmanni, P. glauca, P. sitchensis, Picea* sp., *Pinus contorta, P. ponderosa, Pseudotsuga menziesii, Tsuga heterophylla* (Middlekauff 1960, Kirk 1975, Smith 1979).

Remarks.—This species is known as the "blue horntail." No specimens have been collected in Virginia, but *S. cyaneus* probably occurs in higher elevations in the Appalachians between New York and North Carolina (Amman 1969) where its hosts, *Abies* and *Picea,* occur.

Johnson (1930) recorded hundreds of emergences from balsam fir, *Abies balsamea,* in Randolph, N.H., from July 29 to August 29. He discussed variation in size and color. Forty-one specimens emerged from a section of the tree 11″ long and 4¾″ in diameter. Also, several specimens of *Ibalia* emerged. Amman (1969) reared *S. cyaneus* from Fraser fir in North Carolina. Blackman and Stage (1918), reporting it as *S. abbotii,* reared it from *Larix laricina* in New York.

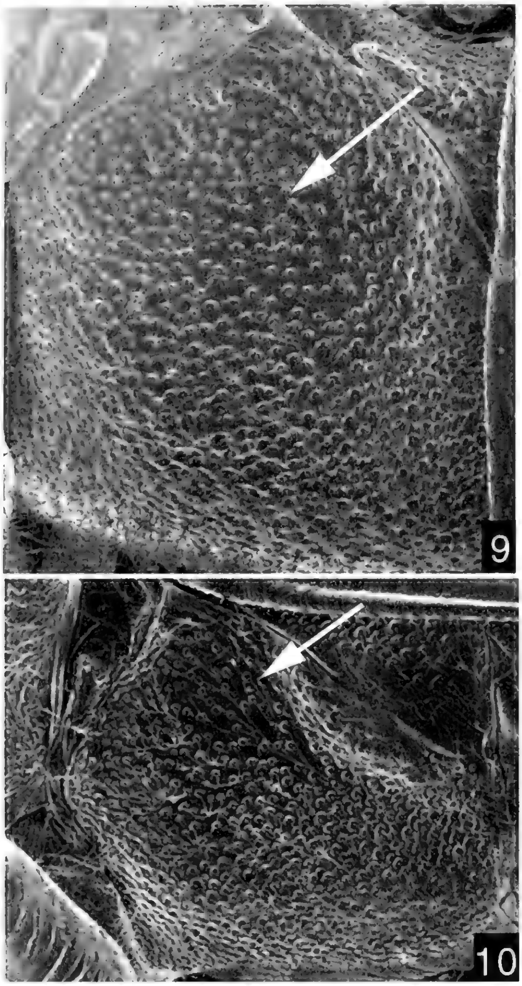
The life history was reported on by Chrystal (1928, 1930) and Chrystal and Meyers (1928). It has often been confused with, or sometimes considered a subspecies of, *S. juvencus.*

Sirex edwardsii Brullé
(Figs. 5, 16)

Distribution.—Alabama, Arkansas, District of Columbia, Georgia, Louisiana, Maryland, Massachusetts, Mississippi, North Carolina, Oklahoma, Quebec, Saskatchewan, South Carolina, Texas, West Virginia, Wisconsin, Virginia. The Louisiana record is from Chapin and Oliver (1986).

Virginia records.—Lynhaven Inl., City of Virginia Beach, X-27-43; Virginia Beach, *Pinus,* Hopk. 69202; W. Minor Hills, Falls Church, pine, Hopk. 11339a1; Montgomery Co., Oct. 2, 1964; Blacksburg, X-11-47.

Collection records.—VIRGINIA: Essex Co., X-24–XI-17-95 (1).



Figs. 9–10. Mesopleuron. 9, *Sirex noctilio.* 10, *Sirex juvencus.* Arrows point to area where density of punctures differ.

Hosts.—*Picea abies; Pinus echinata, P. elliottii, P. palustris, P. rigida, P. strobus, P. virginiana* (Kirk 1974, Smith 1979).

Remarks.—This species was recorded as *Sirex abbotii* by Kirk (1974). In Essex Co., where one specimen was collected, only two species of pines were present (*Pinus virginiana* and *P. taeda*).

Sirex juvencus (Linnaeus)
(Figs. 10, 12)

Distribution.—Eurasia; British Columbia, New Brunswick, Newfoundland (insular and Labrador), New Jersey, Nova Scotia, Yukon Territory.

Hosts.—*Abies balsamea, A. lasiocarpa, Larix* sp., *Picea* sp., *Pinus contorta.*

Remarks.—Benson (1962) first recognized that *S. juvencus* occurs in North America, recording it from "Labrador and Newfoundland (? introduced)." Subsequently, specimens have been identified as *S. juvencus* from across North America, and it is believed to be widespread. Its distinction from *S. cyaneus* and *S. californicus* (Ashmead) is not clear, but we have separated *S. juvencus* and *S. cyaneus* in the key using traditional characters pending a thorough study of this complex.

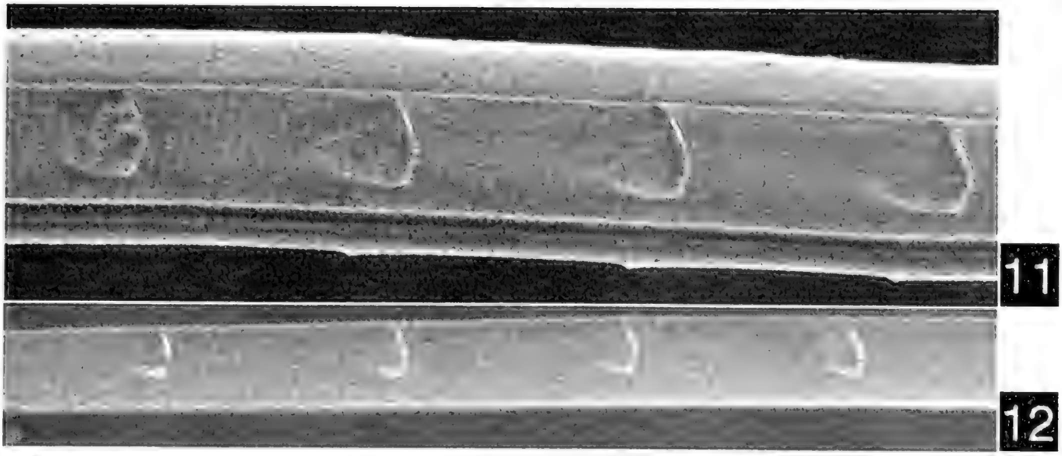
Both *S. juvencus* and *S. cyaneus* can be separated from *S. noctilio,* the three species most likely to be confused, by the much smaller pits on the lancet (Fig. 12; *S. noctilio,* Fig. 11). *Sirex juvencus* and *S. cyaneus* also differ by the size of the pits, with those of *S. cyaneus* being much smaller (breadth of pit less than a third of diameter of ovipositor), but this distinction is not as evident (see Viitasaari and Midtgard 1989).

Sirex longicauda Middlekauff
(Fig. 4)

Distribution.—California, Colorado, Idaho, Kansas, Montana, Nebraska ("emerg. wood in new home;" probably west coast wood), Nevada, New Mexico, Ohio (?), Oregon, Utah, Virginia, West Virginia (Monongalia Co., ex 2 × 4's in new house, lumber cut in Pacific Northwest). Adventive in eastern states emerging from lumber. The records from Kansas, Ohio, and Virginia are probably from imported lumber.

Virginia records.—Campbell Co., Lynchburg, 6-31-64 (1). This specimen is at VPI&SU. Probably emerged from building materials imported from western United States, though this is not given on the labels.

Hosts.—*Abies concolor, A. magnifica; Pinus ponderosa, Pseudotsuga menziesii* (Kirk 1975, Smith 1979).



Figs. 11–12. Pits on lancet. 11, *Sirex noctilio*. 12, *Sirex juvencus*.

Remarks.—So far as is known, this species is not established outside its native range in western North America.

Sirex nigricornis Fabricius
(Figs. 1, 16)

Distribution.—Alabama, Arkansas, District of Columbia, Florida, Georgia, Florida, Louisiana, Maryland, Massachusetts, Mississippi, North Carolina, Ohio, Pennsylvania, Quebec, Saskatchewan, South Carolina, Texas, Virginia, West Virginia, Wisconsin (Kirk 1974, Smith 1979).

Virginia records.—Falls Church, Oct. 14, 1970, Oct. 28, 1916; Virginia Beach, Nov. 11, 1907; Norfolk, 1909; Lurray, Page Co., X-5-13; Lynhaven Inl., City of Virginia Beach, X-27-43; Montgomery Co., X-6-61.

Collection records.—VIRGINIA: Essex Co., IX-29–X-27-92 (1).

Hosts.—*Picea* sp., *Pinus clausa, P. echinata, P. palustris, P. rigida, P. strobus, P. taeda, P. virginiana* (Kirk 1974, Smith 1979).

Remarks.—Webster (1895) received specimens, called the "black horned horntail," reported as being numerous on peach and apple trees in Tennessee. He was probably referring to *S. nigricornis.*

Sirex noctilio (Fabricius)
(Figs. 9, 11)

Distribution.—Eurasia; introduced and established in Australia, New Zealand, Brazil, Uruguay, Argentina, and South Africa.

Hosts.—*Abies* spp., *Larix* spp., *Picea* spp., *Pinus radiata, Pinus* spp., *Pseudotsuga menziesii.*

Remarks.—There is a questionable record for this species in North America by Benson (1962) from "Manitoba (? introduced)." No other information is available and we have not seen confirmed records except the Wyoming record by Smith (1979) from a specimen in the USNM which is labeled "Old Faithful, Yellowstone, Wyo., VIII/26.25, Satterthwait collector." We will not consider this species established in North America until there are more confirmed records. It has been intercepted occasionally in wood and dunnage at ports-of-entry in the United States. This species is a major pest of pine plantations where it has been accidentally introduced (see references in Introduction). We have included it in the preceding key so it can be distinguished from native North American species, and it will be helpful to identifiers at ports-of-entry.

Genus *Urocerus* Geoffroy

Smith (1987) gave a key to North American species. Two species, *Urocerus cressoni* and *U. taxodii,* are widespread in the East, though the latter is seldom collected; one species, *U. albicornis,* is northern and extends south in the Appalachians to North Carolina; one species, *U. gigas flavicornis,* is transcontinental in northern U.S. and Canada; and *U. sah,* an introduced species, has been recorded only from New Hampshire.

KEY TO SPECIES

1\. Female 2
– Male 6
2\. Wings black; antennal flagellum partly white with some basal and/or apical segments black 3
– Wings yellow, only apical margins may be slightly blackish; antenna yellow, scape and pedicel may be black 5
3\. Abdomen mostly red, sometimes basal and/or apical segments blackish . . . . . . *cressoni* Norton
– Abdomen black, only cornus may be orange . . 4
4\. Cornus orange, contrasting with black abdomen; fore- and midlegs usually all black . . . . *taxodii* (Ashmead)
– Cornus black; basal half of tibiae and basal half of tarsi of each leg whitish yellow . . . . *albicornis* (Fabricius)
5\. Yellow on head continuous across top, at most separated by a narrow black line at center of postocellar area; pronotum and upper half of mesepisternum yellowish orange (legs mostly yellow with hindfemur and apical two-thirds of hindtibia black) . . . . *sah* (Mocsáry)
– Yellow on head separated into a spot on each side by a black band usually as broad as distance between eyes; thorax black . . . . *gigas flavicornis* (Fabricius)
6\. Head mostly yellow to yellow orange; wings yellowish (legs usually with hindfemur and apical two-thirds of hindtibia black; apical abdominal segment may be black) . . *sah* (Mocsáry)
– Head largely black, with a broad black band separating yellow spots on each side of head; wings blackish or hyaline 7
7\. Abdomen reddish, may be black at base, but basically unicolorous; wings black 8
– Abdominal segments 1 and 2 or 1 to 3, and 7 to apex black, segments 2 or 3 to 7 red to orange; wings hyaline 9
8\. Legs black . . . . *cressoni* (Norton)
– Fore- and midtibiae and tarsi dark orange; basal third of hindtibia and basal half of hindbasitarsus white . . . . *taxodii* (Ashmead)
9\. Hindbasitarsus 4.0–5.5 × longer than broad . . . . *gigas flavicornis* (Fabricius)
– Hindbasitarsus 6.5–8.0 × longer than broad . . . . *albicornis* (Fabricius)

Urocerus albicornis (Fabricius)

Distribution.—British Columbia, California, Georgia, Idaho, Louisiana, Michigan, Minnesota, Missouri, Montana, New Brunswick, Newfoundland, New Mexico, New York, North Carolina, Nova Scotia, Ontario, Oregon, Pennsylvania, Rhode Island, Virginia, Washington, West Virginia.

Virginia records.—Montgomery Co., VIII-8-74; Arlington, VI-10-1952; Washington Co., Bristol, 7-24-72.

Hosts.—*Abies amabilis, A. balsamea, A. fraseri, A. lasiocarpa; Larix laricina, L. occidentalis; Picea engelmanni, P. mariana, P. sitchensis; Pinus* spp.; *Pseudotsuga menziesii; Thuja plicata; Tsuga heterophylla* (Smith 1978).

Remarks.—Some of the Virginia records may represent emergence from imported lumber or firewood in buildings; the species is probably native to only the higher elevations. For the life cycle, see Belyea (1952). Amman (1969) reared this species from Fraser fir, *Abies fraseri,* in North Carolina. Blackman and Stage (1918) reared it from *Larix laricina* in New York and gave notes on its life history; it was found in dying or recently felled conifers.

Urocerus cressoni Norton
(Figs. 2, 6, 16)

Distribution.—Florida, Georgia, Iowa, Minnesota, Nebraska, New Brunswick, North Carolina, Nova Scotia, Ohio, Ontario, Quebec, Virginia, Wisconsin.

Virginia records.—Falls Church, IX-2-17; Montgomery Co., VIII-9-1974.

Collection records.—VIRGINIA: Essex Co., VII-27–VIII-9-91 (1), VIII-27–IX-16-91 (1); VII-3–16-96 (1); VII-17–VIII-2-96 (2); VII-18–VIII-1-97 (4); VIII-2–18-97 (2); IX-9–X-6-97 (2); VII-4–21-98 (3); VIII-22–IX-11-98 (3); IX-12–X-5-98 (1);

VII-17–VIII-2-99 (3); VIII-3–20-99 (3). Fairfax Co., IX-16–22-90 (1).

Hosts.—*Abies balsamea, A. fraseri; Picea* sp.; *Pinus rigida, P. taeda* (Kirk 1974, Smith 1979).

Remarks.—Most all collections in Essex Co., VA, were from traps in or adjacent to mixed coniferous hardwood forests. The predominant conifers were *Pinus taeda* and *P. virginiana.* All collections were from July to early October (Fig. 16). Sixteen of the 26 specimens from this collection had no white behind the eyes or a very small and faint white spot slightly lighter than the black on the rest of the head; thus, they could be confused with *Sirex* if the female cornus and male hind tarsus are not checked carefully.

Bradley (1913) recognized several varieties based on the amount of red on the abdomen and wing darkness: (1) abdomen entirely red and wings dark fuliginous; (2) basal six dorsal segments of abdomen dark brown; and (3) abdomen red with a black band on the third, fourth, and fifth dorsal segments. All specimens collected would belong to variety (2), except three had the basal 5 segments black, one had the basal 7 segments black, and one had only the basal 3–4 segments black. In a number of specimens, there is a central red mark on the second segment.

Amman (1969) reared this species from Fraser fir, *Abies fraseri,* in North Carolina.

Urocerus gigas flavicornis (Fabricius)

Distribution.—Alaska, Alberta, Arizona, California, Colorado, Idaho, Montana, New Mexico, Northwest Territories, Ontario, Oregon, Washington, Wyoming, Yukon Territory.

Hosts.—*Abies concolor, A. lasiocarpa, Larix occidentalis, Picea engelmanni, P. sitchensis, Pinus contorta, Pseudotsuga menziesii* (Middlekauff 1960, Kirk 1975).

Remarks.—The North American form is considered a subspecies of the Eurasian *Urocerus gigas* (Linnaeus). It is transcontinental in Canada, but we have not seen specimens from eastern United States.

Urocerus sah (Mocsáry)

Distribution.—North Africa, Asia Minor and the Near East, southern Russia; New Hampshire.

Hosts.—Probably *Abies* spp., *Picea* spp., *Pinus* spp.

Remarks.—This species was first recorded in North America by Smith (1987) from several specimens taken in New Hampshire. No other specimens have been discovered. It is close to the European *Urocerus augur* (Klug) and sometimes has been treated as a subspecies of it.

Urocerus taxodii (Ashmead)
(Fig. 16)

Distribution.—District of Columbia, Florida, Mississippi, Missouri, Virginia.

Virginia records.—City of Virginia Beach, Cape Henry, VI-8-24.

Collection records.—VIRGINIA: Essex Co., V-14–24-91 (1).

Host.—*Taxodium distichum* (Smith 1979).

Remarks.—It was unusual to find a specimen in Essex Co., VA. No *Taxodium* were anywhere near the trap in which it was collected.

Genus *Xeris* Costa

Xeris spectrum (Linnaeus)
(Figs. 7, 8)

Distribution.—Holarctic; Alaska, Arizona, British Columbia, California, Colorado, Connecticut, Maine, Michigan, Montana, Nevada, New Brunswick, New Hampshire, Nova Scotia, Oregon, Utah, Washington.

Hosts.—*Abies concolor, A. lasiocarpa, Larix occidentalis, Picea engelmanni, P. pungens, Pinus contorta, P. ponderosa, Pseudotsuga menziesii. Pinus contorta* is the favorite host in California (Middlekauff 1960, Kirk 1975).

Remarks.—This species is transcontinental in Canada and northern United States.

The most southern records in the East are Connecticut and Michigan. Adults of this species mate at the highest points on mountain tops. Many specimens were hand collected at the top of Mount Rigaud, Quebec (H. Goulet, personal communication).

Subfamily Tremicinae

Genus *Tremex* Jurine

Tremex columba (Linnaeus)

(Fig. 15)

Distribution.—Alabama, Arizona, Arkansas, California (one record from Riverside Co.), Colorado, Connecticut, Georgia, Florida, Illinois, Indiana, Iowa, Kansas, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Brunswick, New Jersey, New Mexico, New York, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, Tennessee, Texas, Utah, Virginia, West Virginia, Wisconsin, Wyoming (Middlekauff 1960, Smith 1979).

Virginia records.—Widespread throughout the state. We have seen specimens from the following: Appomattox Co., Arlington Co., Bedford Co., City of Norfolk, Clarke Co., Essex Co., Fairfax Co., Frederick Co., Giles Co., Hanover Co., Louisa Co., Loudoun Co., Montgomery Co., Nottaway Co., Roanoke Co., Smythe Co., Warren Co., Washington Co.

Collection records.—MARYLAND: Prince George's Co. (4). VIRGINIA: Clarke Co. (12); Essex Co. (84); Fairfax Co. (7); Loudoun Co. (11); Louisa Co. (19). WEST VIRGINIA: Tucker Co. (3). See Fig. 15 for dates of collection.

Hosts.—*Acer* spp., *Ulmus* spp., *Quercus* spp., *Carya* spp., *Fagus grandifolia, Fagus* spp. (Smith 1979); *Celtis laevigata, Carpinus* sp. Also reared or collected from the following: apple, box elder, hackberry, pear, and sycamore (Middlekauff 1960). Probably in other angiospermous trees. Usually in dead or dying trees.

Remarks.—This species is known as the "pigeon tremex." Adults oviposit in dead or weakened deciduous trees or those dying as a result of disease or other cause. Feeding of larvae in the wood aids in the disintegration of trees. Stillwell (1967) noted a minimum two year life cycle in New Brunswick where the primary host was weakened or injured *Fagus grandifolia,* and occasionally *Acer saccharum.* Adult emergence and oviposition was from August to October, and 2–7 eggs were laid in each oviposition hole. Eggs hatched in 2–4 weeks or hatched the next May or June. Larvae tunnel in wood infected with the fungus *Daedalea unicolor,* a fungus associated with each stage of the female development. Stillwell (1965) also studied the hypopleural organs in larvae and the associated fungus. Eggs in absence of the fungus hatch but larvae do not develop past the first instar. Oviposition tunnels are at a right angle to the bark surface and 2–15 mm deep in the sapwood; eggs are laid at intervals along the tunnel. Several hundered eggs are deposited at intervals in the gallery. Packed sawdust and frass are in the galleries. Galleries may be 1–2 m long. Pupation is in the sapwood or up to 30 cm deep in the heartwood and may be oriented in any direction. The females may tunnel up to 1 m before emergence.

Laurent (1931) found numerous larvae in dead or nearly dead maple during May in Pennsylvania. From a cross section of trunk, 20″ long and 10″ in diameter, 96 males and 10 females emerged June 16–26; 7 males and 22 females from June 27 to July 6; 5 females and 1 female from July 7–16; and about the same number through August. There were no specimens after August. In all, 162 *Tremex* emerged.

Fattig (1949) observed *Megarhyssa* (Ichneumonidae) parasitoids in Georgia. From a dead tree, 86 specimens of *Megarhyssa* emerged during July. From July 29 to August 22, he collected 28 specimens of *T. columba.* He reported his observations on oviposition of the parasitoid.

Harrington (1887) gave some biological notes for *T. columba* on maple in Ontario.

Fig. 13. *Eriotremex formosanus.*

This species is extremely variable in coloration of the body and wings. Because of this, Bradley (1913) recognized several color races: (1) Entire body fulvous, legs beyond femora yellow, and wings dark reddish brown; (2) abdomen marked with black and yellow with ground color black and wings brown or yellowish; and (3) abdomen marked with black and yellow with ground color yellow and wings yellow. From collections of 133 specimens, 21% corresponded with variety (1) with the body entirely dark yellowish and the wings darkly and almost uniformly black, and 79% corresponded with variety (2) having the abdomen mostly black with yellow bands which vary in size. All had blackish wings, but some were slightly paler than others. This second form (2) is the predominate form in the northeastern states, while the pale form (1) is most common in the southeastern states.

Genus *Eriotremex* Maa

Eriotremex formosanus (Matsumura)

(Fig. 13)

Distribution.—Alabama, Georgia, Florida, Louisiana, Mississippi, North Carolina, South Carolina, Texas, Virginia (Smith 1996).

Virginia records.—City of Virginia Beach, Seashore State Park, maintenance area, 30-X-1989.

Hosts.—*Quercus nigra*; *Q. phellos*; *Carya* sp. Also recorded from dead oak trees, laurel oak, in trunk of *Quercus alba*, firewood of *Liquidambar styraciflua*, dead hickory, and firewood of water oak. Adult collection records, mostly from label data,

Fig. 14. *Ibalia anceps,* lateral.

are on *Quercus laurifolia, Liquidamber styraciflua, Pinus palustris, Pinus taeda,* "on bark of longleaf pine" (*Pinus palustris*), "ovipositor imbedded in slash pine" (*Pinus elliottii*), "sitting on *Pinus taeda.*"

Remarks.—See Smith (1996) for distribution and spread of this species in the United States. Most adult collection records are from April to June and September to November. Very few have been collected in July, August, December, and February.

Eriotremex formosanus may be confused with *Tremex columba.* In *E. formosanus,* the antennae are 20–21 segments (14–15 in *T. columba*), there are dense long golden hairs on the head and body (short and not as bright or grayish in *T. columba*), and the color pattern is consistent, with the pronotum and band on the abdomen yellow and the wings hyaline with their apices infuscated and with a dark spot below the stigma (Fig. 13) (variable in *T. columba,* but not with this color pattern).

Ibaliidae

Genus *Ibalia* Latreille

Liu and Nordlander (1992) gave a key to the severn North American species and Liu and Nordlander (1994) keyed the 13 world species. The genus is Holarctic, with two species in the eastern United States.

KEY TO SPECIES

1. Abdomen red; head and thorax black . . . . *leucospoides* (Hockworth)
– Orange yellow with black stripes or markings (Fig. 14) . . . . *anceps* Say

Ibalia anceps Say
(Figs. 14, 15)

Distribution.—Arkansas, Colorado, Florida, Georgia, Illinois, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Brunswick, New Jersey, New York, Nova Scotia, Ontario, Pennsylvania, Tennessee, Texas, Virginia, West Virginia, Wisconsin.

Virginia records.—The only records are from the collections below.

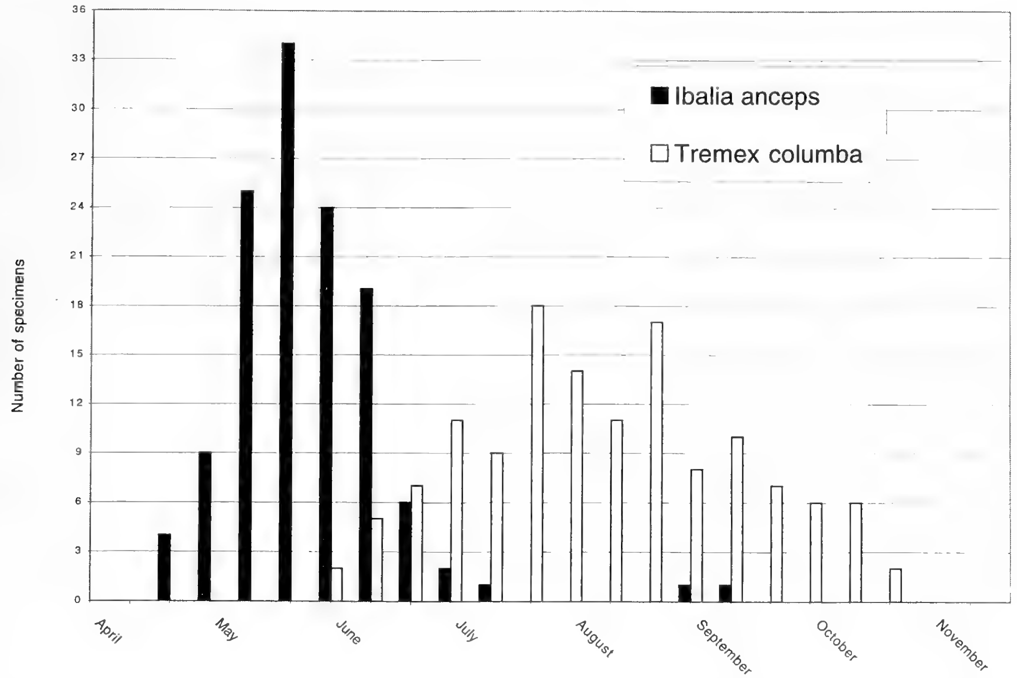


Fig. 15. Seasonal occurrence of *Ibalia anceps* and *Tremex columba* from collections in Maryland, Virginia, and West Virginia.

Collection records.—MARYLAND: Allegheny Co. (9); Prince George's Co. (28). VIRGINIA: Clarke Co. (9); Essex Co. (45); Fairfax Co. (4); Loudoun Co. (7). WEST VIRGINIA: Hardy Co. (7); Tucker Co. (17). All collections are from the end of April to the first of July with the peak flight time from mid-May to mid-June. The two records in September are from Allegheny Co. See Fig. 15 for flight times.

Host.—A parasitoid of *Tremex columba* in deciduous trees (Liu and Nordlander 1994).

Remarks.—Adult flight activity is limited to spring, whereas *Tremex columba* flies from July through October (Fig. 15). Since *T. columba* takes two or more years to complete its life cycle, the *Ibalia* possibly parasitizes the young larvae from eggs laid by the *Tremex* from the previous year.

Liu and Nordlander (1994) recognized variation in wing and body coloration of this species. The three predominate wing color forms are: (1) wings maculate with dark and almost clear areas; (2) same, but more or less dark; and (3) evenly dark. The first is the most common in the northeastern states, and all specimens collected appear to be of this form (Fig. 14).

Ibalia leucospoides (Hochworth)
(Fig. 16)

Distribution.—Europe; Alberta, Arizona, California, Colorado, Florida, Georgia, Idaho, Maine, Maryland, Michigan, Minnesota, Mississippi, New Brunswick, North Carolina, Oregon, Pennsylvania, South Carolina, Utah, Virginia, Washington, West Virginia.

Virginia records.—City of Virginia Beach, Cape Henry, IX-18-23.

Collection records.—VIRGINIA: Essex Co. IV-9–21-94 (1), IV-12–26-95 (2), X-24–XI-17-95 (1), IX-28–X-23-95 (1), VIII-19–IX-8-97 (1), IX-9–X-6-97 (3), X-7–31-97 (1), VIII-4–21-98 (1), VIII-22–IX-11-98 (2), IX-12–X-5-98 (3), X-6–XI-7-98 (1); Fairfax Co. VII-12–16-82 (1), VII-6-85

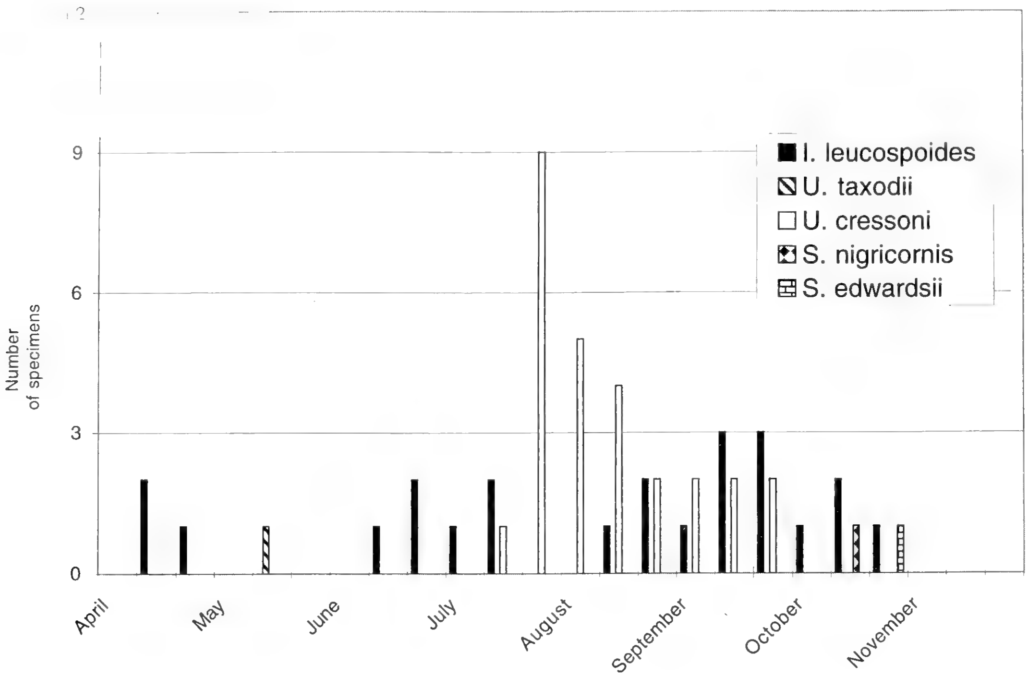


Fig. 16. Seasonal occurrence of *Ibalia leucospoides* and *Sirex edwardsii, S. nigricornis, Urocerus cressoni,* and *U. taxodii* from collections in Maryland, Virginia, and West Virginia.

(1), VII-8–14-85 (1), IX-6–12-98 (1); Louisa Co. VI-29-85 (1), VI-8–19-89 (1), VI-22–VII-3-89 (1).

Hosts.—A parasitoid of woodwasps of the genera *Sirex, Urocerus,* and *Xeris* living in various conifers (Liu and Nordlander 1994).

Remarks.—Chrystal (1930) studied this species in Europe. Eggs are inserted in the egg of the host before hatching or on the first larval instar. They hatch after 2–3 months to a year later. The third stage leaves the interior of the host larva and starts to tunnel toward the surface of the log. Pupation is 5–6 weeks. The complete life cycle is not less than three years. Adults were found from August to October ovipositing in spruce and larch infested with *Sirex cyaneus.*

Kirk (1974) collected this species from trees infested with *Sirex edwardsii* (as *abbotii*) and *S. nigricornis* in Alabama, Georgia, South Carolina, and Florida. Infested trees included *Pinus virginiana, P. taeda, P. clausa, P. elliottii,* and *P. palustris.*

In the mid-Atlantic states, adults were collected from April to October, with most from August to October (Fig. 16). There was no clear, narrow emergence time as for *Ibalia anceps,* and correlations with the emergence times of the host siricids could not be determined.

HOST LIST FOR SIRICIDAE OF EASTERN UNITED STATES

Abies amabilis Douglas ex J. Forges (Pacific silver fir).—*Urocerus albicornis.*

Abies balsamea (L.) Mill. (balsam fir).—*Sirex cyaneus, S. juvencus, Urocerus albicornis, U. cressoni.*

Abies concolor (Gord. & Glend.) Lindl. ex F.H. Hildebr. (white fir).—*Sirex cyaneus, S. longicauda, Urocerus gigas flavicornis, Xeris spectrum.*

Abies fraseri (Pursh) Poir. (Fraser fir).—

Sirex cyaneus, Urocerus albicornis, Urocerus cressoni.

Abies grandis (Douglas ex. D. Don) Lindl. (grand fir).—*Sirex cyaneus.*

Abies lasiocarpa (Hook.) Nutt. (subalpine fir).—*Sirex cyaneus, S. juvencus, Urocerus albicornis, Urocerus gigas flavicornis, Xeris spectrum.*

Abies magnifica A. Murray (California red fir).—*Sirex cyaneus, S. longicauda.*

Abies sp. (fir).—*Sirex noctilio, Urocerus sah.*

Acer negundo L. (boxelder).—*Tremex columba.*

Acer spp. (maple).—*Tremex columba.*

Carpinus sp. (hornbeam).—*Tremex columba.*

Carya spp. (hickory).—*Tremex columba, Eriotremex formosanus.*

Celtis laevigata Willd. (lowland hackberry).—*Tremex columba.*

Cupressus macrocarpa Hartw. ex Gordon (Monterey cypress).—*Sirex areolatus, S. behrensii.*

Fagus grandifolia Ehrh. (American beech).—*Tremex columba.*

Fagus spp. (beech).—*Tremex columba.*

Juniperus occidentalis Hook. (western juniper).—*Sirex areolatus.*

Juniperus scopulorum Sarg. (Rocky Mountain juniper).—*Sirex areolatus.*

Larix laricina (Du Roi) K. Koch (tamarack).—*Sirex cyaneus, Urocerus albicornis.*

Larix occidentalis Nutt. (western larch).—*Urocerus albicornis, U. gigas flavicornis, Xeris spectrum.*

Larix sp. (larch).—*Sirex juvencus, S. noctilio.*

Libocedrus decurrens Torr. (incense-cedar).—*Sirex areolatus.*

Liquidamber styraciflua L. (sweetgum).—*Eriotremex formosanus.*

Picea abies (L.) Karst (Norway spruce).—*Sirex edwardsii.*

Picea engelmanni Parry (Engelmann spruce).—*Sirex cyaneus, Urocerus albicornis, U. gigas flavicornis, Xeris spectrum.*

Picea glauca (Moench) Voss (white spruce).—*Sirex cyaneus.*

Picea mariana (Mill.) B.S.P. (black spruce).—*Urocerus albicornis.*

Picea pungens Engelm. (blue spruce).—*Xeris spectrum.*

Picea sitchensis (Bong.) Carr. (sitka spruce).—*Sirex cyaneus, Urocerus albicornis, U. gigas flavicornis.*

Picea sp. (spruce).—*Sirex cyaneus, S. juvencus, S. nigricornis, S. noctilio, Urocerus cressoni, U. sah.*

Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg. (sand pine).—*Sirex nigricornis.*

Pinus contorta Douglas ex Loudon (lodgepole pine).—*Sirex areolatus, S. cyaneus, S. juvencus, Urocerus gigas flavicornis, Xeris spectrum.*

Pinus echinata Mill. (shortleaf pine).—*Sirex edwardsii, S. nigricornis.*

Pinus elliottii Engelm. (slash pine).—*Sirex edwardsii.*

Pinus jeffreyi Grev. & Balf. (Jeffrey pine).—*Sirex areolatus, S. behrensii.*

Pinus lambertiana Dougl. (sugar pine).—*Sirex areolatus.*

Pinus palustris Mill. (longleaf pine).—*Sirex edwardsii, S. nigricornis.*

Pinus ponderosa Dougl. ex Laws. (ponderosa pine).—*Sirex behrensii, S. cyaneus, S. longicauda, Xeris spectrum.*

Pinus radiata D. Don (Monterrey pine).—*Sirex areolatus, S. behrensii, S. noctilio.*

Pinus rigida Mill. (pitch pine).—*Sirex edwardsii, S. nigricornis, Urocerus cressoni.*

Pinus strobus L. (eastern white pine).—*Sirex edwardsii, S. nigricornis.*

Pinus taeda L. (loblolly pine).—*Sirex nigricornis, Urocerus cressoni.*

Pinus virginiana Mill. (Virginia pine).—*Sirex edwardsii, S. nigricornis.*

Pinus sp. (pine).—*Sirex noctilio, Urocerus albicornis, U. sah, Eriotremex formosanus* (?).

Platanus occidentalis L. (sycamore).—*Tremex columba.*

Pseudotsuga menziesii (Mirb.) Franco (Douglas-fir).—*Sirex areolatus, S. cy-*

[illegible]*us, S. longicauda, S. noctilio, Urocerus albicornis, U. gigas flavicornis, Xeris spectrum.*

Pyrus sp. (apple, pear).—*Tremex columba.*

Quercus alba L. (white oak).—*Eriotremex formosanus.*

Quercus laurifolia Michx. (laurel oak).—*Eriotremex formosanus.*

Quercus nigra L. (water oak).—*Eriotremex formosanus.*

Quercus phellos L. (willow oak).—*Eriotremex formosanus.*

Quercus sp. (oak).—*Tremex columba, Eriotremex formosanus.*

Sequoia sempervirens (D. Don) Engl. (redwood).—*Sirex areolatus.*

Taxodium distichum (L.) Rich. (baldcypress).—*Sirex areolatus, Urocerus taxodii.*

Thuja plicata Donn ex D. Don (western redcedar).—*Urocerus albicornis.*

Thuja sp. (cedar).—*Sirex areolatus.*

Tsuga heterophylla (Raf.) Sarg. (western hemlock).—*Sirex cyaneus, Urocerus albicornis.*

Ulmus spp. (elm).—*Tremex columba.*

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NEW *ALISOTRICHIA* (TRICHOPTERA: HYDROPTILIDAE) FROM CENTRAL AND SOUTH AMERICA AND THE GREATER ANTILLES

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Abstract.—Twelve new species of *Alisotrichia,* ***A. panamensis, A. woldai, A. linterna, A. asta,*** and ***A. cuernita*** from Panama, ***A. neblina*** and ***A. viuda*** from Venezuela, ***A. muellita*** from Peru, ***A. kanukua*** from Guyana, ***A. cacaulandia*** from Brazil, and ***A. mathisi*** and ***A. paxilla*** from Jamaica are described and illustrated. A new record of *A. timouchela* Botosaneanu from Venezuela is also provided.

Key Words: Trichoptera, Hydroptilidae, *Alisotrichia,* new species, Neotropics

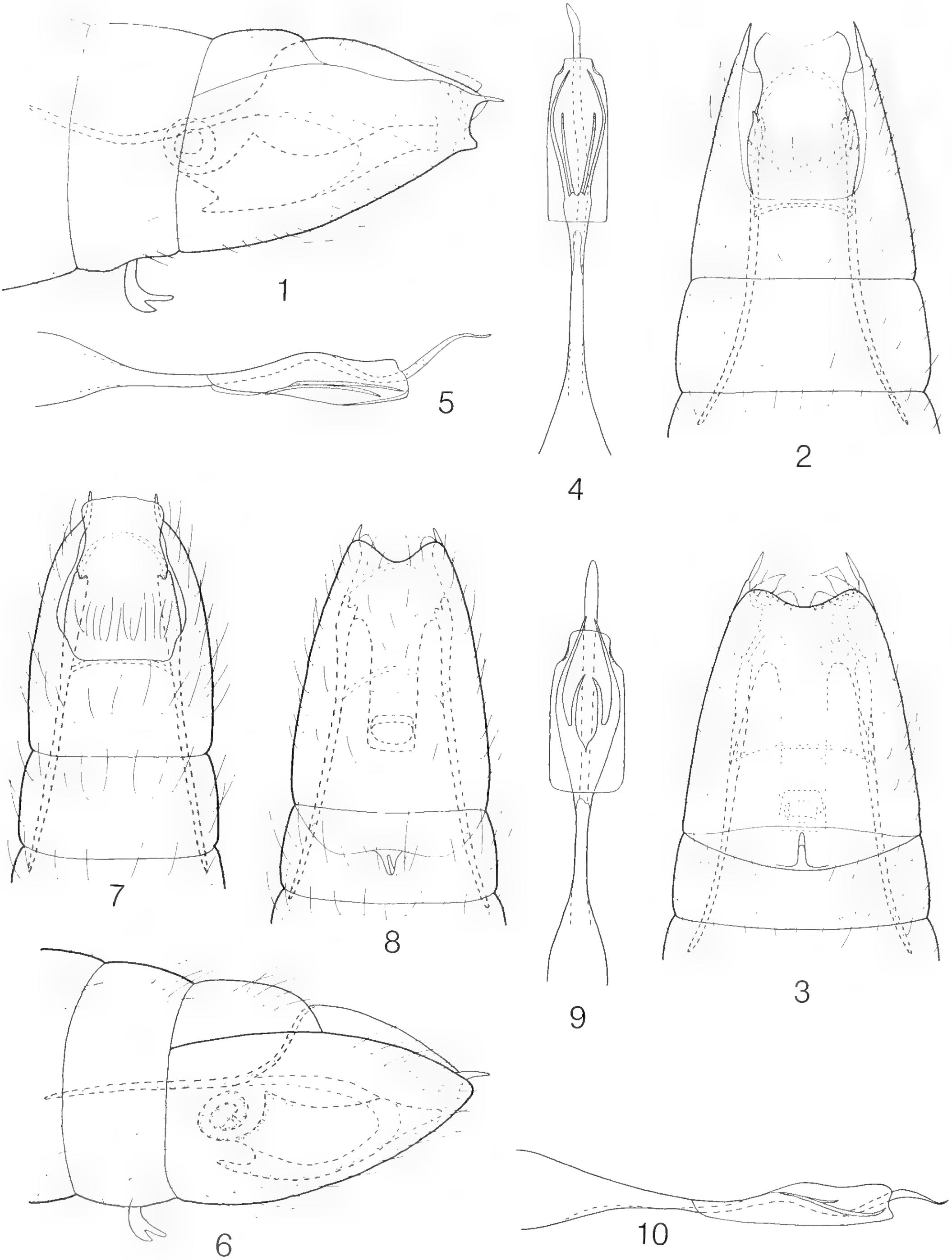
The genus *Alisotrichia* is widespread throughout Mexico, Central America, northern South America and the West Indies. There are currently 33 species and subspecies, including one fossil species from Dominican amber, assigned to the genus (Flint et al. 1999). This paper describes 12 additional species, primarily from Panama, but also from Venezuela, Peru, Guyana, Brazil, and Jamaica.

Harris and Holzenthal (1993) divided the 32 then known species of *Alisotrichia* into eight monophyletic species groups. Since then, the three basal groups have been elevated to full generic status: the former *A. blantoni* Group as *Mejicanotrichia* Harris and Holzenthal, the former *A. dominicensis* Group as *Cerasmatrichia* Flint, Harris and Botosaneanu, and the former *A. quemada* Group as *Scelobotrichia* Harris and Bueno. Nine of the new species herein described are being placed in the *A. orophila* Group. *Alisotrichia woldai, A. cacaulandia, A. kanukua, A. mathisi, A. paxilla,* and *A. neblina* agreeing in all characteristics of that group. *Alisotrichia panamensis* and *A. muellita* although lacking the dorsal process and macroseta of segment VIII, agree with several other species in the group in the possession of the spring-like process of the venter of segment X and together with *A. linterna* in the ventral process of segment VII and internal structure of the phallus. One species, *A. viuda,* is tentatively placed in the *A. hirudopsis* Group based on the two pairs of apical processes from segment VIII. The final two species, *A. asta* and *A. cuernita,* based on the presence of elaborate lobes from the dorsolateral margin of segment VIII are placed in the *A. chorra* Group.

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

Alisotrichia panamensis
Harris and Flint, new species
(Figs. 1–5)

In many respects this species is very similar to *A. muellita,* n.sp., from Peru and *A.*



Figs. 1–10. Male genitalia. 1–5, *Alisotrichia panamensis.* 1, Lateral. 2, Dorsal. 3, Ventral. 4, Phallus, ventral. 5, Phallus, lateral. 6–10, *A. muellita.* 6, Lateral. 7, Dorsal. 8, Ventral. 9, Phallus, ventral. 10, Phallus, lateral.

woldai, n.sp., also from Panama. In common with these species, as well as *A. circinata* Flint from Puerto Rico, *A. panamensis* has a single spring-like structure anteroventrally from segment X and lying within the eighth sternite. *Alisotrichia panamensis* is distinguished from these other species on the basis of the presence of a elongate apicodorsal process from the eighth segment and from *A. woldai* and *A. circinata* in lacking the dorsal setate process from the eighth sternum.

Male.—Length 1.8–1.9 mm. Antenna cream colored, black at tip with 18 segments, scape greatly enlarged and setose. Head and thorax with central mass of white hair dorsally. Forewing with extensive white hairs, black on margin, with diffuse black bands or spots. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII roughly rectangular in lateral view, truncate posteriorly with elongate dorsolateral process, and short, lobate ventrolateral process; in ventral view longer than wide, with shallow mesal incision distally. Segment IX short, incomplete ventrally, apparently fused with X dorsally. Tergum X concave posteriorly in dorsal aspect, anteriorly with pair of slender apodemes extending through segment VII; highly modified tubular structure attached to venter of these apodemes and elaborately coiled anteriorly (this structure appears to be loosely attached to venter of X, as it will move anteriorly and posteriorly). Phallus wide basally, tubular sheath posteriorly enclosing two pairs of slender lateral rods which originate at the same level, lateralmost rods longer than inner rods; slender ejaculatory duct protruding tongue-like beyond sheath.

Female.—Unknown.

Type material.—Holotype, ♂: Panama, Barro Colorado Island, Canal Zone, July 1967, W. W. Wirth, Malaise trap. Paratypes: same data as holotype, 1 ♂; same, but Snyder-Molino trail, marker 3, light trap III, 19–25 August 1987, H. Wolda, 1 ♂; same, but 25 November–1 December 1987, 1 ♂; same, but 9–15 December 1987, 1 ♂; same, but 2–8 November 1988, 1 ♂; same, but 23–29 November 1988, 1 ♂; same, but 11–17 January 1989, 2 ♂; same, but 29 November–5 December 1989, 1 ♂; same, but 2–8 January, 1991, 1 ♂; same, but light trap I, 4–10 November 1987, 1 ♂; same, but 2–8 January 1988, 1 ♂; same, but 28 December 1988–3 January 1989, 1 ♂; same, but 6–12 December 1989, 3 ♂; same, but 13–19 December 1989, 2 ♂; same, but 3–9 January 1990, 1 ♂.

Etymology.—Named for the country of Panama.

Alisotrichia muellita Harris and Flint, new species

(Figs. 6–10)

This is another species of the group possessing a spring-like structure from the venter of segment X. *Alisotrichia muellita* is very similar to *A. panamensis* differing primarily in the structure of the phallic rods which are united basally into an enlarged plate and the shape of the eighth segment that is conical apically with an elongate process projecting from the inner dorsal margin.

Male.—Length 1.7–1.9 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, scape greatly enlarged and setose. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII narrowing to rounded apex in lateral view, with elongate process projecting from inner posterodorsal margin; in ventral view longer than wide, shallow mesal incision distally. Segment IX short, incomplete ventrally, apparently fused with X dorsally. Tergum X rounded posteriorly, anteriorly with pair of slender apodemes extending through segment VII; 1 highly modified tubular structure attached to venter of these apodemes and elaborately coiled anteriorly. Phallus wide basally, tubular sheath posteriorly enclosing two pairs of thin lateral rods, lateralmost rods about twice length inner rods, inner rods originating from mesal margins of lateral rods;

slender ejaculatory duct protruding tongue-like beyond sheath.

Female.—Unknown.

Type material.—Holotype, ♂: Peru, Madre de Dios, Manu, Pakitza, 11°56′S, 71°18′W, el. 250 m, 12–18 September 1989, N. Adams et al., kitchen stream, Malaise trap, night collection. Paratypes: same data as holotype, 2 ♂.

Etymology.—Spanish, "small spring," referring to the structure within segment VIII.

Alisotrichia woldai Harris and Flint, new species

(Figs. 11–15)

Although similar to *A. muellita* in the structure of the phallus, and *A. panamensis* in the shape of segment VIII, *A. woldai* appears to be more closely related to *A. circinata* in the presence of seta-bearing processes from the dorsal margin of segment VIII. In common with all of these species, *A. woldai* has a spring-like structure within sternum VIII. *Alisotrichia woldai* is distinguished from these other species on the basis of the lateralmost pair of phallic rods which arise from a large, rectangular base.

Male.—Length 1.4–1.7 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, scape greatly enlarged and setose. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII tapering posteriorly to truncate apex in lateral view, anterodorsally with seta-bearing process on each side; in ventral view rectanguloid with wide mesal incision distally, forming inwardly hooked lobes laterally. Segment IX elongate dorsally and apparently fused with X, incomplete ventrally. Tergum X thin with mesal incision posteriorly, anteriorly with pair of slender apodemes originating from ventrolateral margin IX + X and extending anteriorly through segment VII; highly modified spring-like structure attached to the venter of these apodemes. Phallus wide basally, tubular sheath posteriorly enclosing two pairs of sclerotized rods, lateralmost rods longer than inner rods and widened at base, inner rods thin over length and originating from base of lateral rods; slender ejaculatory duct protruding tongue-like beyond sheath.

Female.—Unknown.

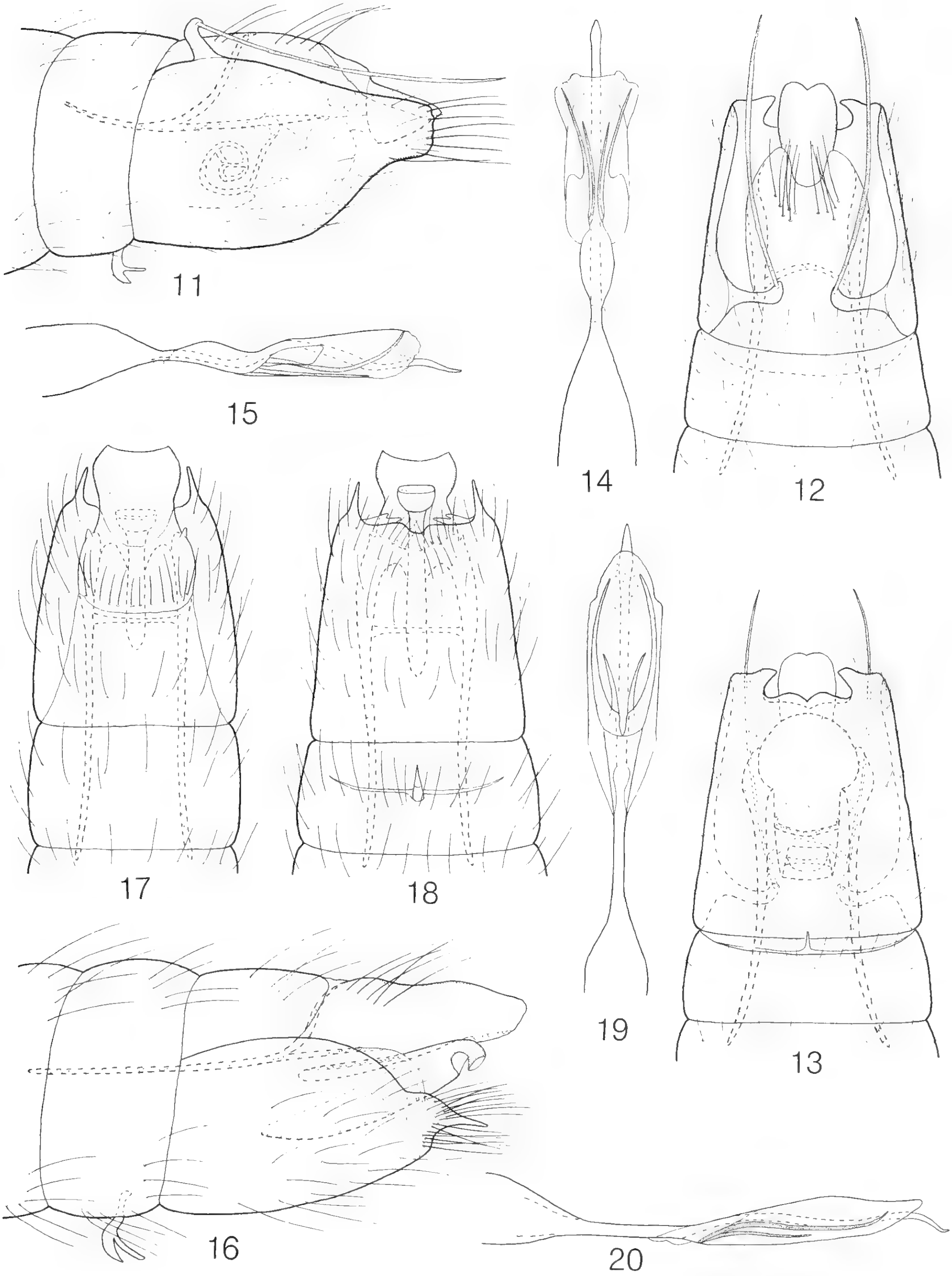
Type material.—Holotype, ♂: Panama, Barro Colorado Island, Snyder-Molino trail, marker 3, light trap I, 7–13 December 1988, H. Wolda. Paratypes: same data as holotype, but 21–27 December 1988, 1 ♂; same, but 26 September–2 October 1990, 1 ♂; same, but light trap III, 28 October–3 November 1987, 1 ♂; same, but 28 December 1988–3 January 1989, 1 ♂; same, but 2–8 January 1991, 1 ♂.

Etymology.—Named for Dr. Henk Wolda, who collected most of the Panama material.

Alisotrichia linterna Harris and Flint, new species

(Figs. 16–20)

This new species is difficult to place. In some respects, notably the structure of the phallus, *A. linterna* is similar to the preceding species, but it lacks the spring-like structure from the venter of segment X. Instead, this species has a tubular structure, which is similar to the three following new species, *A. cacaulandia* n.sp. from Brazil, *A. kanukua* n.sp. from Guyana, and *A. mathisi* n.sp. from Jamaica. It is possible, although difficult to verify, that all of these species are united by the presence of the development of the venter of segment X, the structure of this development simply varying from species to species, spring-like in some, tubular in others. From *A. panamensis, A. muellita,* and *A woldai, A. linterna* differs in the lack of the spring-like process, and from *A. cacaulandia, A. kanukua,* and *A. mathisi* in the lack of a pair of dorsal setigerous lobes from segment VIII. Both *A. linterna* and *A. mathisi* have a ventromesal process from segment VII, but the phallus of *A. linterna* bears two pairs on internal spines which are lacking in *A. mathisi.*



Figs. 11–20. Male genitalia. 11–15, *Alisotrichia woldai.* 11, Lateral. 12, Dorsal. 13, Ventral. 14, Phallus, ventral. 15, Phallus, lateral. 16–20, *A. linterna.* 16, Lateral. 17, Dorsal. 18, Ventral. 19, Phallus, ventral. 20, Phallus, lateral.

Male.—Length 1.8 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, scape greatly enlarged and setose. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII tapering posteriorly in lateral view to acute apical process; in ventral view square with shallow mesal incision and lateral margins produced into acute spine-like projections. Segment IX short and fused with X, incomplete ventrally. Tergum X an elongate lobe in lateral view, in dorsal view rounded laterally and concave apically, anteriorly with pair of slender apodemes originating from ventrolateral margin IX + X and extending through segment VII; venter of X with elongate tubular structure, downturned and pipe-like posteriorly, capitate in ventral view. Phallus wide basally, tubular sheath posteriorly enclosing two pairs of slender lateral rods, lateralmost rods over twice length inner rods, inner rods originating from mesal bases of lateral rods; slender ejaculatory duct protruding tongue-like beyond sheath.

Female.—Unknown.

Type material.—Holotype, ♂: Panama, Barro Colorado Island, Snyder-Molino trail, marker 3, light trap I, 23–29 November 1988, H. Wolda.

Etymology.—Spanish "flashlight," referring to the distinctive shape of the ventral process within segment VIII.

Alisotrichia cacaulandia Harris and Flint, new species

(Figs. 21–25)

This new species is most closely related to *A. kanukua* from Guyana. Both have elongate tubular phalli, both have seta-bearing processes from segment VIII, and both have a tubular process running through segment VIII, but probably attached to the venter of X. *Alisotrichia cacaulandia* is separated from *A. kanukua* on the basis of the scoop-shaped eighth segment, and the extra ventral process from X within this segment.

Male.—Length 1.9 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, scape greatly enlarged and setose. Middle legs with linear tufts of hair along femora. Abdominal segment VII annular, without ventromesal process. Segment VIII tapering posterodorsad in lateral view, anterodorsally with pair of process each bearing elongate seta; in ventral view longer than wide with mesal and lateral incisions distally, in dorsal view widening posterior of seta-bearing processes. Segment IX short and fused with X, incomplete ventrally. Tergum X oval, anteriorly with pair of slender apodemes originating from ventrolateral margin of IX + X and extending through segment V; venter of IX + X with an elongate tubular structure, downturned and pipe-like posteriorly, and bearing linear rod ventrally. Phallus slender and tubular, with ejaculatory duct protruding distally.

Female.—Unknown.

Type material.—Holotype, ♂: Brazil, Rondonia, creek 8 km S Cacaulandia, light trap, 21 November 1991, D. Petr.

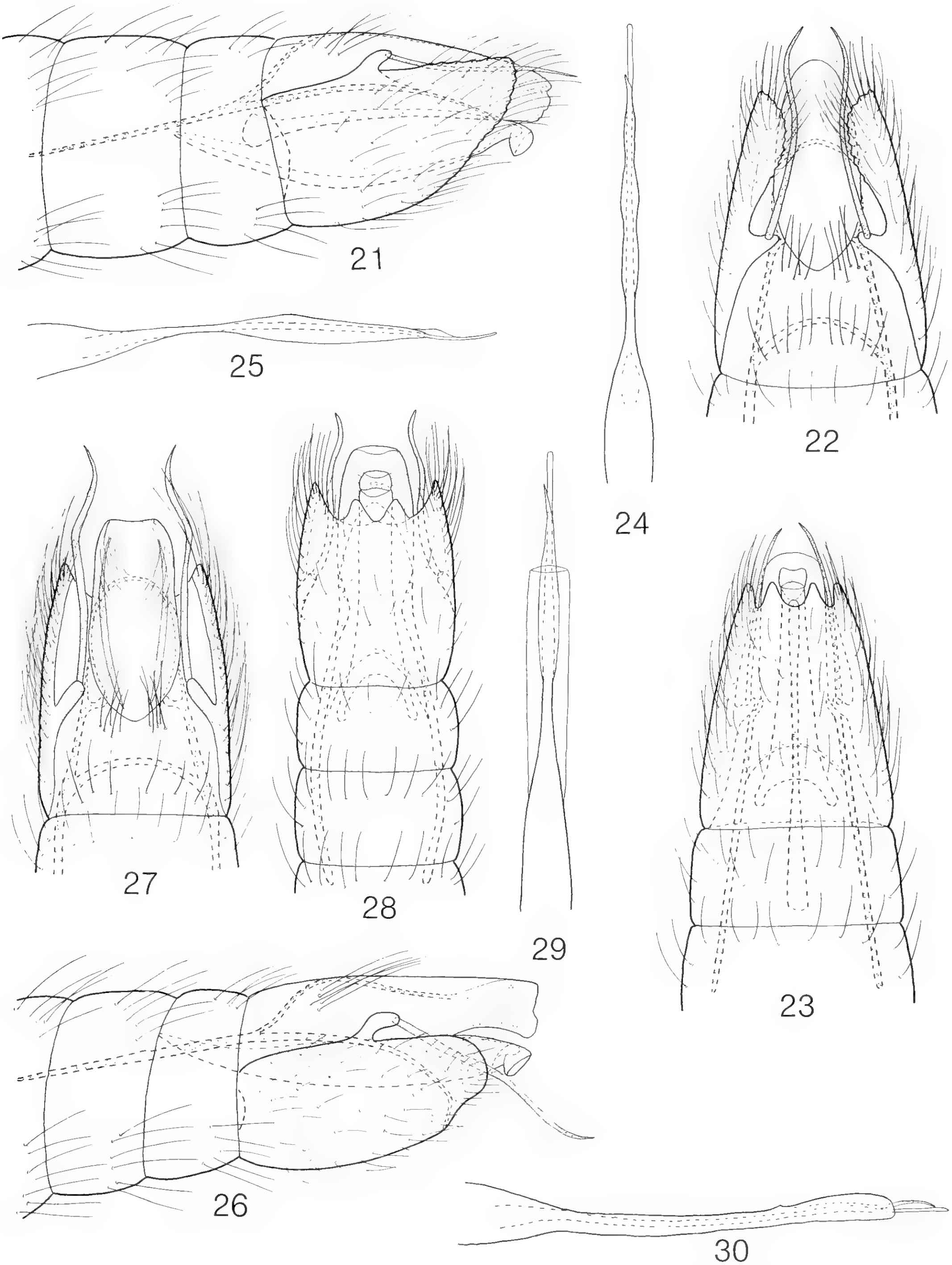
Etymology.—Named for the locality of the type specimen.

Alisotrichia kanukua Harris and Flint, new species

(Figs. 26–30, 63–65)

This new species is most closely related to the previous species, *A. cacaulandia,* differing in the rounded shape of the eighth segment in lateral aspect and in the structure of the process from the venter of segment IX + X which lacks the linear ventral rod.

Male.—Length 1.8–2.0 mm. Head and antenna brown, antennal scape greatly enlarged and spatulate, 18 segments. Thorax brown, dorsally with mesal, white, longitudinal stripe. Forewing brown with white, longitudinal stripe basally, white, transverse band at midlength, and scattered white spots posteriorly. Abdominal segment VII annular, without ventromesal process. Segment VIII oval, slightly tapering posteriorly to rounded apex in lateral view, anterodorsally with pair of process



Figs. 21–30. Male genitalia. 21–25, *Alisotrichia cacaulandia.* 21, Lateral. 22, Dorsal. 23, Ventral. 24, Phallus, ventral. 25, Phallus, lateral. 26–30, *A. kanukua.* 26, Lateral. 27, Dorsal. 28, Ventral. 29, Phallus, ventral. 30, Phallus, lateral.

each bearing elongate seta; in ventral view square with single mesal and paired lateral incisions distally. Segment IX short and fused with X, incomplete ventrally. Tergum X rectangular, anteriorly with pair of slender apodemes originating from ventrolateral margin IX + X and extending through segment V; dorsally with pair of parenthesis-like sclerites; venter of IX + X with elongate tubular structure, downturned and pipe-like posteriorly. Phallus slender and tubular, with ejaculatory duct protruding distally; tubular sheath surrounding distal portion of phallus.

Female.—Length 1.9–2.2 mm. Coloration as in male. Antenna with 17 segments, scape enlarged slightly and rounded. Abdominal segment VI as wide as long, tapering posteriorly. Segment VII rectangular with ring of setigerous lobes on posterior margin; dorsum with elongate mesal process. Segment VIII short, with pair of lateral apodemes originating near junction with segment IX and extending anteriorly into segment V. Segment IX rectangular, with pair of lateral apodemes extending anteriorly into segment VII. Segment X cone-shaped, with pair of posterolateral papillae. Bursa copulatrix small and plate-like with attached lateral wings, and with very long, mesal process extending posteriad.

Type material.—Holotype, ♂: Guyana, Kanuku Mountains, Moco River, 3°18.2′N, 59°38.9′W, 29 April 1995, O. S. Flint, Jr. Paratypes: same data as holotype, 22 ♂, 20 ♀. Moco-Moco, 10 km E Lethem, 3°18.2′N, 59°39.0′W, 3–6 April, 1994, O. S. Flint, Jr., 4 ♂.

Etymology.—Named for the type locality, the Kanuku Mountains, in southern Guyana.

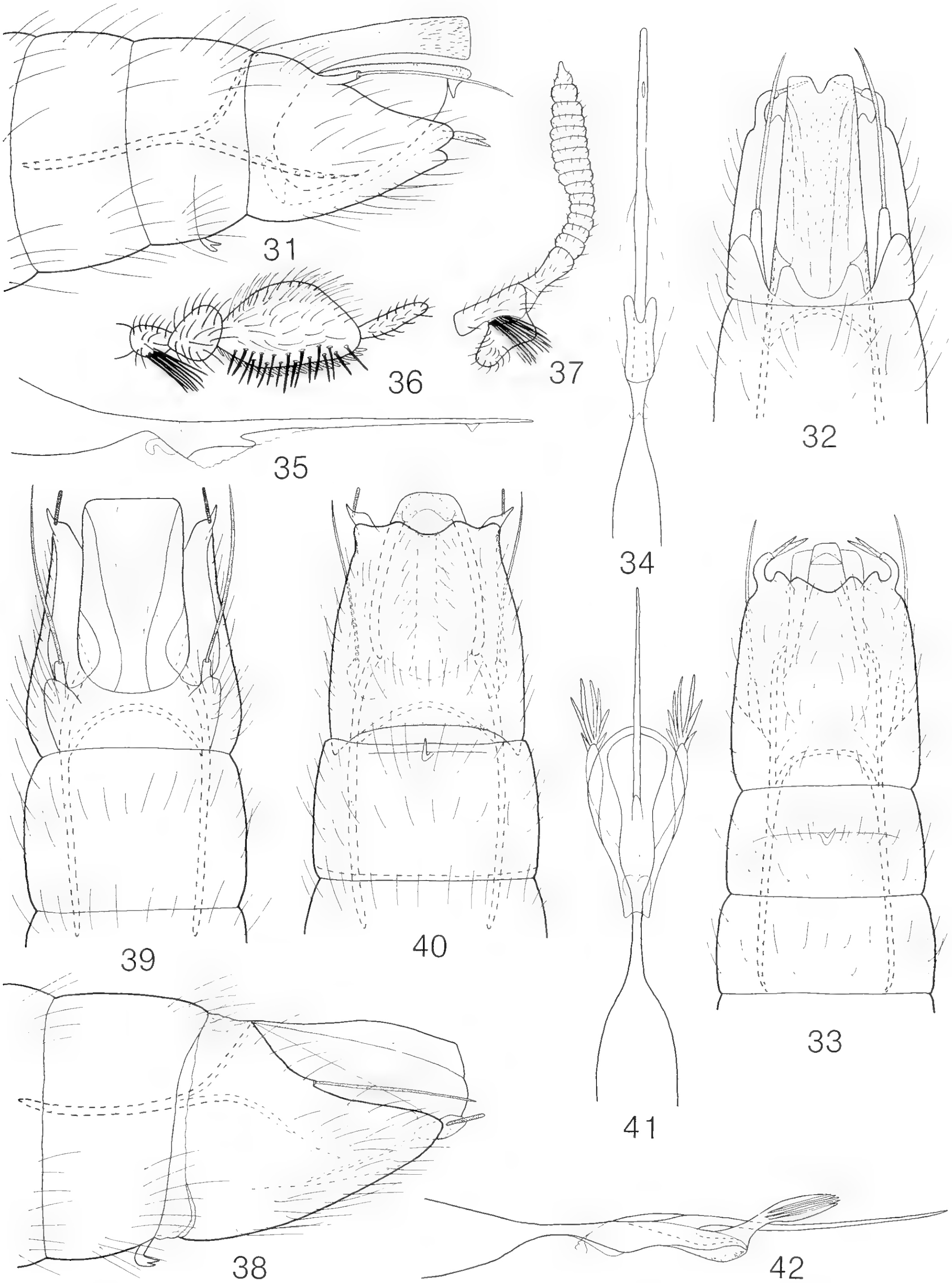
Alisotrichia mathisi Harris and Flint, new species

(Figs. 31–37, 68)

Alisotrichia mathisi is similar to the previous two species based on the development of the venter of segment X and in possession of a simple tubular phallus. From both *A. cacaulandia* and *A. kanukua, A. mathisi* differs in the presence of a ventromesal process from segment VII and in having a spinose process from segment VIII which is similar to that seen in *A. orophila* Flint and *A. paxilla.* From these latter two species, *A. mathisi* may be distinguished by the shape of the segment VIII spine and from *A. paxilla* by the very differently formed phallus.

Male.—Length 2.0 mm. Head brown with profuse white hairs dorsally, antenna light brown with scape enlarged, distal segments slightly widened, maxillary palps with subterminal segment greatly enlarged and bearing numerous stout setae on outer margin. Thorax brown, dorsally with patches of white hair on sides and middle. Forewing brown with longitudinal stripe of white hair on anterior margin, which widens distally and curves inward, several white spots on posterior margin and basally. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII triangular in lateral view, apically shallowly bilobed, dorsal lobe bearing bifid spine, dorsolaterally with paired slender processes each bearing elongate seta; square in ventral view, with shallow mesal incision posteriorly, lateral process thin and curving inwardly, bearing bifid spine. Segment IX short and fused with X dorsally, incomplete ventrally. Tergum X rectanguloid, mesal notch distally, pair of sclerotized bands on lateral margins; pair of slender apodemes originating at anterolateral margins and extending through segment VI; in lateral view with structure at mid-height with flat dorsal margin and rounded ventral margin, apex turned downward and beak-like, tubular in ventral view. Phallus slender, with small bilobed structure just above mesal constriction, subapically with thin, triangular lamella protruding from venter.

Female.—Length 2.0–2.2 mm. Coloration as in male. Antenna with 17 segments, scape enlarged slightly and rounded. Ab-



Figs. 31–42. 31–37, *Alisotrichia mathisi,* male. 31, Genitalia, lateral. 32, Same, dorsal. 33, Same, ventral. 34, Phallus, ventral. 35, Phallus, lateral. 36, Maxillary palpus, mesal. 37, Antenna, anterior. 38–42, *A. paxilla,* male genitalia. 38, Lateral. 39, Dorsal. 40, Ventral. 41, Phallus, ventral. 42, Phallus, lateral.

dominal segment VI as wide as long, tapering posteriorly. Segment VII rectangular with ring of setiferous lobes on posterior margin; dorsum with elongate mesal process. Segment VIII short, with pair of lateral apodemes originating near junction with segment IX and extending anteriorly into segment V. Segment IX rectangular, with pair of lateral apodemes extending anteriorly into segment VII. Segment X conical, with pair of posterolateral papillae. Bursa copulatrix thin and elongate, membranous and folded accordion-like anteriorly, posteriorly conical, with sclerotized lateral margins, internally with slender, elongate rod, which extends posteriorly.

Type material.—Holotype, ♂: Jamaica, St. Andrew, Mavis Bank (1.7 km E), Yallahs River, 18°2.4′N, 77°39.5′W, el. 575 m, 1 May 2000, W. N. Mathis. Paratypes: Same data, 1 ♂; same, but 21–22 April 2000, 2 ♂, 1 ♀. 4.3 km SE Mavis Bank, Yallahs River, 18°1.4′N, 76°38.1′W, el. 480 m, 22–23 April 2000, 2 ♂, 4 ♀. St. Thomas, Bath Fountain Spring, 17°57.6′N, 76°21.3′W, 15 May 1996, D. & W. Mathis, H. Williams, 2 ♀.

Etymology.—Named for Dr. Wayne N. Mathis, who collected all the material of this species while sweeping for shore flies.

Alisotrichia paxilla Harris and Flint, new species

(Figs. 38–42, 69)

Alisotrichia paxilla is the second new species from Jamaica, and very similar to the previously described *A. mathisi.* Males of both species have segment VIII terminating in a heavy spine, both have tergum X with sclerotized margins, and both have an elongate, slender phallus. However, the phallus of *A. paxilla* has a complex median structure which bears numerous spines, and the posterior spine from segment VIII is peg-like rather than bifid and acute, as seen in *A. mathisi.* Although the females of the two species are similar, both having a simple, thin bursa copulatrix, *A. paxilla* does not have the accordion-like, anterior, membranous section.

Male.—Length 1.5–1.8 mm. Brown in alcohol. Antenna with 16 segments, scape enlarged. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII triangular in lateral view, dorsolaterally with pair of slender processes each bearing elongate seta, posteroventrally with inner process bearing peg-like spine; apex square in ventral view, with shallow posteromesal emargination, posterolateral processes acute and angling outward, each bearing peg-like spine. Segment IX narrow and fused with X dorsally, incomplete ventrally; pair of slender apodemes originating laterally and extending anteriad through VII. Tergum X rectanguloid, dorsally with pair of sclerotized bands on lateral margins, narrow membranous lobe mesally; in lateral view rectanguloid with ventral portion lobate; in ventral view with tubular mesal process, sclerous laterally, and narrow, distal bridge bearing numerous tubercles. Phallus slender with complex process originating at mesal constriction and bearing cluster of elongate spines laterally.

Female.—Length 1.9–2.1 mm. Coloration as in male. Antenna with 13 segments, scape enlarged slightly and rounded. Abdominal segment VI as wide as long, tapering posteriorly. Segment VII rectangular with ring of setiferous lobes on posterior margin; dorsum with elongate mesal process. Segment VIII short, with pair of lateral apodemes originating near junction with segment IX and extending anteriorly into segment VII. Segment IX rectangular, with pair of lateral apodemes extending anteriorly into segment VII. Segment X conical, with pair of posterolateral papillae. Bursa copulatrix narrow and elongate, membranous anteriorly with slender mesal sclerite, posteriorly with long, slender process, tapering apicad, bifid basally.

Type material.—Holotype, ♂: Jamaica, St. Elizabeth, Elim, 18°7.1′N, 77°40.5′W, 14 April 2000, C. M. & O. S. Flint, Jr. Paratypes: Same data, 2 ♂, 2 ♀.

Etymology.—Latin, "peg," referring to the distinctive spine from apex of segment VIII.

Alisotrichia neblina Harris and Flint, new species

(Figs. 43–47, 66–67)

This new species does not appear to be closely related to any of the known *Alisotrichia* species. Like many of the species described from islands of the Caribbean, *A. neblina* has the dorsal seta-bearing processes from segment VIII, but it lacks the ventral spines from this segment, typical of these species.

Male.—Length 1.3 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, scape enlarged and setose, but not covering front of face as in most species. Abdominal segment VII annular, without ventromesal process. Segment VIII mitten-shaped in lateral view, anterodorsally with pair of processes each bearing elongate seta; in ventral view longer than wide with mesal incision distally; in dorsal view short tapering caudad with narrow lateral margin posteriad of seta-bearing process. Segment IX short, anteriorly with slender apodeme originating from ventrolateral angle and extending into segment VII. Tergum X tapering in lateral view, square in dorsal view; venter of IX + X with tongue-like process protruding beyond segment VIII. Phallus wide basally, posteriorly with tubular sheath bearing series of short spines apically, internally with forked, sclerotized rod; ejaculatory duct tongue-like and protruding distally.

Female.—Length 1.4–1.6 mm. Coloration as in male. Antenna with 17 segments, scape enlarged slightly and rounded. Abdominal segment VI as wide as long, tapering posteriorly, dorsally with median sclerotized projection. Segment VII rectangular with ring of setigerous lobes on posterior margin; dorsum with elongate mesal process. Segment VIII short, with pair of lateral apodemes originating near junction with segment IX and extending anteriorly into segment V. Segment IX rectangular, with pair of lateral apodemes extending anteriorly into segment VII. Segment X cone-shaped, with pair of posterolateral papillae. Bursa copulatrix oval with slender anterior process, internally with rectangular plate, membranous posteriorly.

Type material.—Holotype, ♂: Venezuela, Territorio Federal Amazonas, Cerro de la Neblina, basecamp, 0°50′N, 66°10′W, el. 140 m, flight intercept trap across small stream in forest, 24 February 1985, P. J. and P. M. Spangler, R. Faitoute, W. Steiner. Paratypes: same data as holotype, 2 ♀.

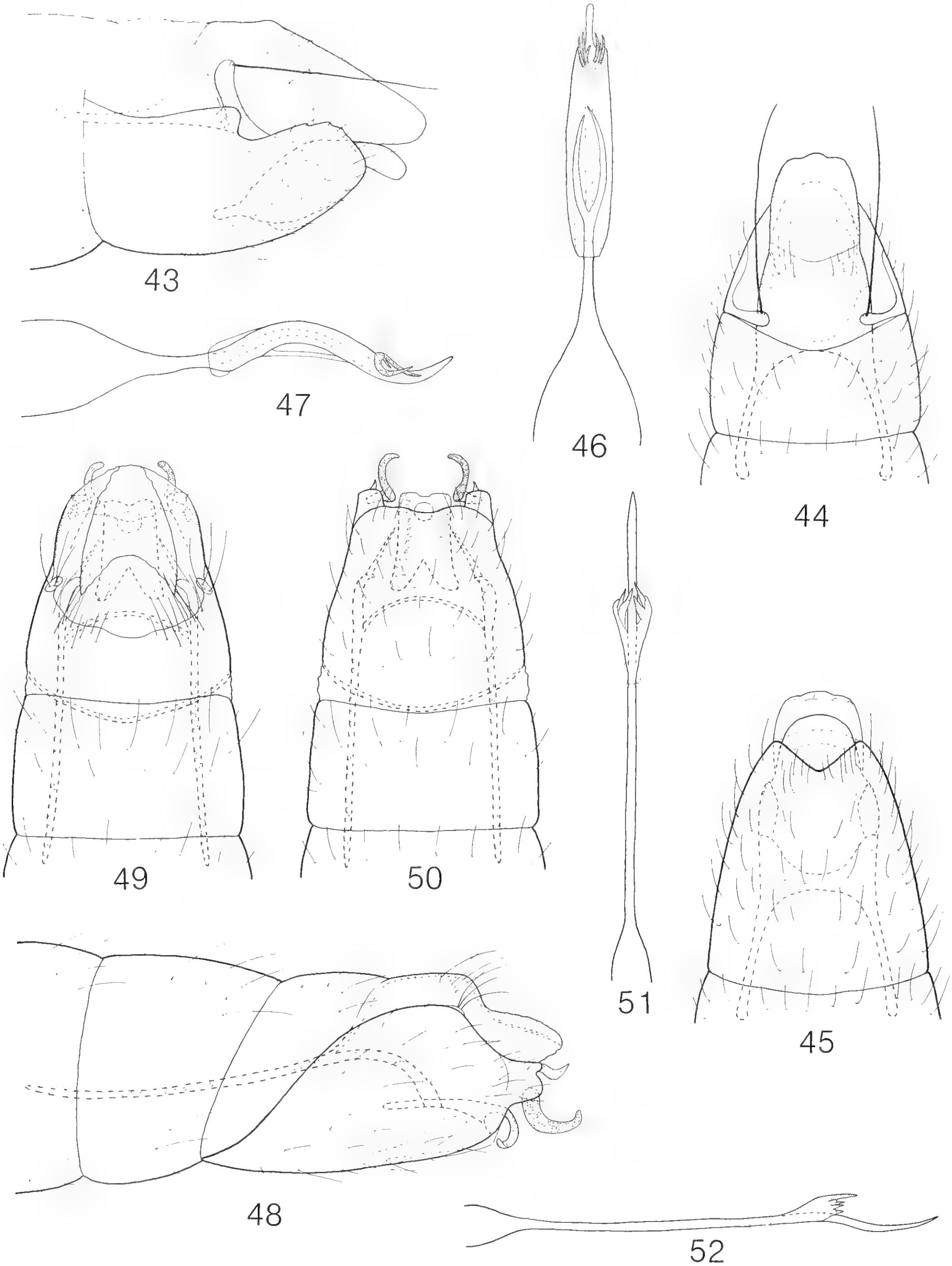
Etymology.—Named for the locality of the type specimen.

Alisotrichia viuda Harris and Flint, new species

(Figs. 48–52)

This second new species from Venezuela appears to be most similar to *A. chiquitica* Botosaneanu or *A. alayoana* Botosaneanu, which are known from Cuba, particularly in the possession of two pairs of sclerotized processes from the apex of segment VIII. *Alisotrichia viuda* is separated by the lack of the pair of parenthesis-like bars on the dorsum of the segment X and by bearing a series of spines subapically from the phallus.

Male.—Length 1.4 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, flagellum with segments of basal half slightly widened, scape greatly enlarged and setose. Abdominal segment VII annular, without ventromesal process. Segment VIII widest at midlength, tapering anteriorly and posteriorly in lateral view, distally produced into truncate lobe bearing two sclerotized processes, upper process short and spinous, lower process elongate and upturned apically; dorsal margin with small, setiferous knob; apex in ventral view nearly square, with distal, sclerotized-pro-



Figs. 43–52. Male genitalia. 43–47, *Alisotrichia neblina*. 43, Lateral. 44, Dorsal. 45, Ventral. 46, Phallus, ventral. 47, Phallus, lateral. 48–42, *A. viuda*. 48, Lateral. 49, Dorsal. 50, Ventral. 51, Phallus, ventral. 52, Phallus, lateral.

cess curved mesad. Segment IX incomplete ventrally, dorsally fused with segment X. Tergum X a lobate shelf posteriorly, anteriorly produced into a pair of slender apodemes which extend into segment VI, in dorsal view a membranous lobe; venter of X sclerotized, shelf-like in lateral view, with downward curving process distally, in ventral view appearing rectanguloid. Phallus slender, elongate, wide basally and subapically, which bears a series of stout spines; ejaculatory duct slender, extending beyond spinous apex.

Female.—Unknown.

Type material.—Holotype, ♂: Venezuela, Sucre, Parque Nacional Peninsula de Paria, Uquire, Rio La Viuda, 10°42.83′N, 61°57.66′W, el. 15 m, 30 March–1 April 1995, Malaise trap, day and night, R. Holzenthal, O. Flint, and C. Cressa.

Etymology.—Named for the Rio La Viuda, locality of the type specimen.

Alisotrichia asta Harris and Flint, new species

(Figs. 53–57)

This species and the following form a closely related group, which appear to be most similar to *A. chorra* Flint on the basis of an elaborate process from the dorsal margin of segment VIII. *Alisotrichia asta* may be recognized by the structure of this process, and the simplicity of the phallus.

Male.—Length 1.8 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, flagellum with segments of basal half slightly widened, scape greatly enlarged and setose. Middle leg with cluster of long hairs from its tibia. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII, tapering posteriorly in lateral view to an acute apex, anterodorsally with small, setate lobe, posterodorsally with thin sclerotized process, deeply serrate on posterodorsal surface; in ventral view rounded, apex with mesal incision; in dorsal view, with dorsolateral setate plates, flared sclerotized processes distally. Segment IX short and band-like dorsally, incomplete ventrally. Segment X truncate, shelf-like posteriorly, anteriorly produced into a pair of thin apodemes which extend through segment VIII; tergum cone-like, with lateral margins lightly sclerotized. Phallus slender and elongate, wide basally and submesally; apex slender and whip-like in lateral view.

Female.—Unknown.

Type material.—Holotype, ♂: Panama, Barro Colorado Island, Snyder-Molino trail, marker 3, light trap III, 23–29 November 1988, H. Wolda.

Etymology.—Spanish word for "antler," referring to the distinctive processes from segment VIII.

Alisotrichia cuernita Harris and Flint, new species

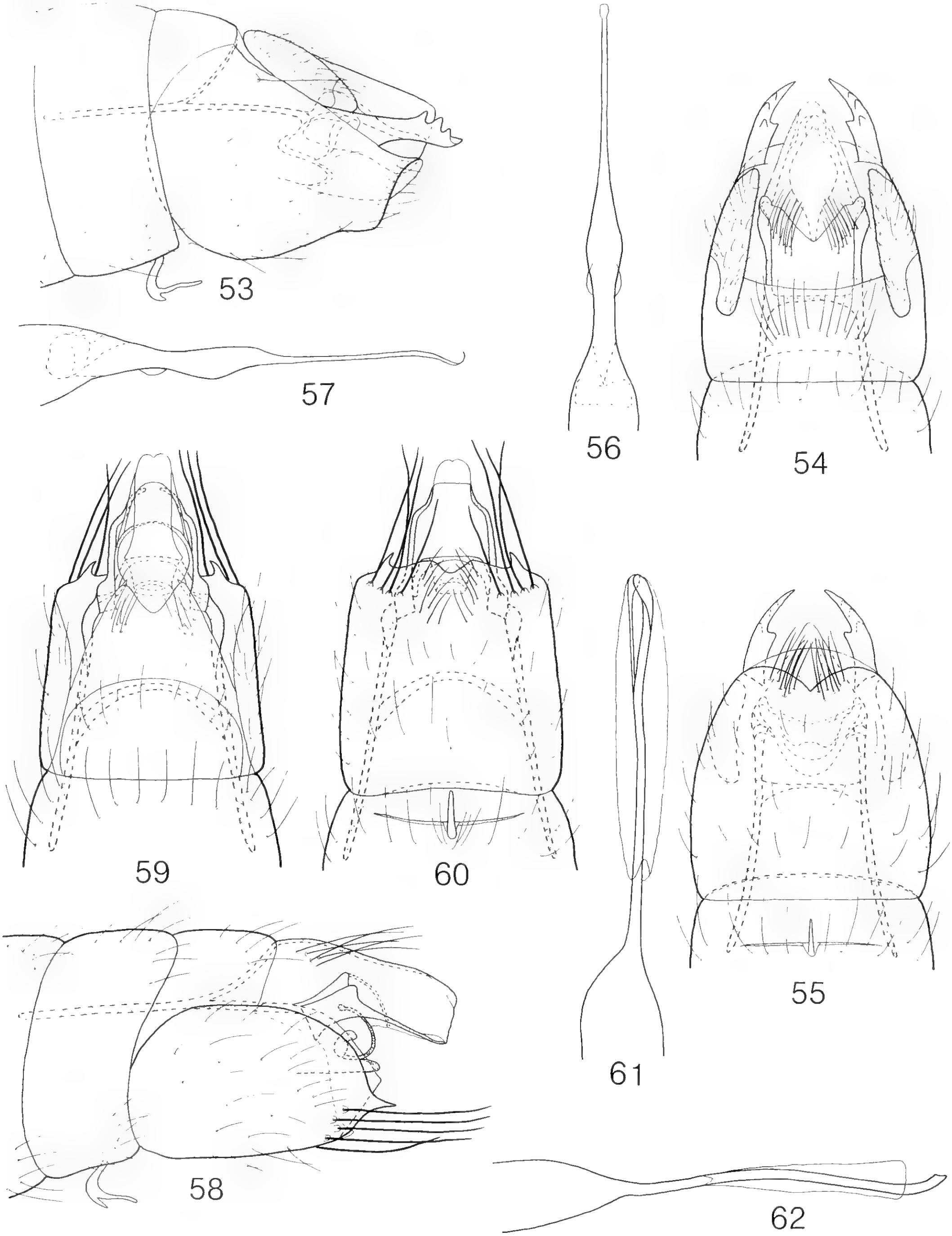
(Figs. 58–62)

Most closely related to *A. asta,* this species, also from the former Canal Zone in Panama, is easily distinguished by the elaborate process from the dorsum of segment IX and structure of the phallus.

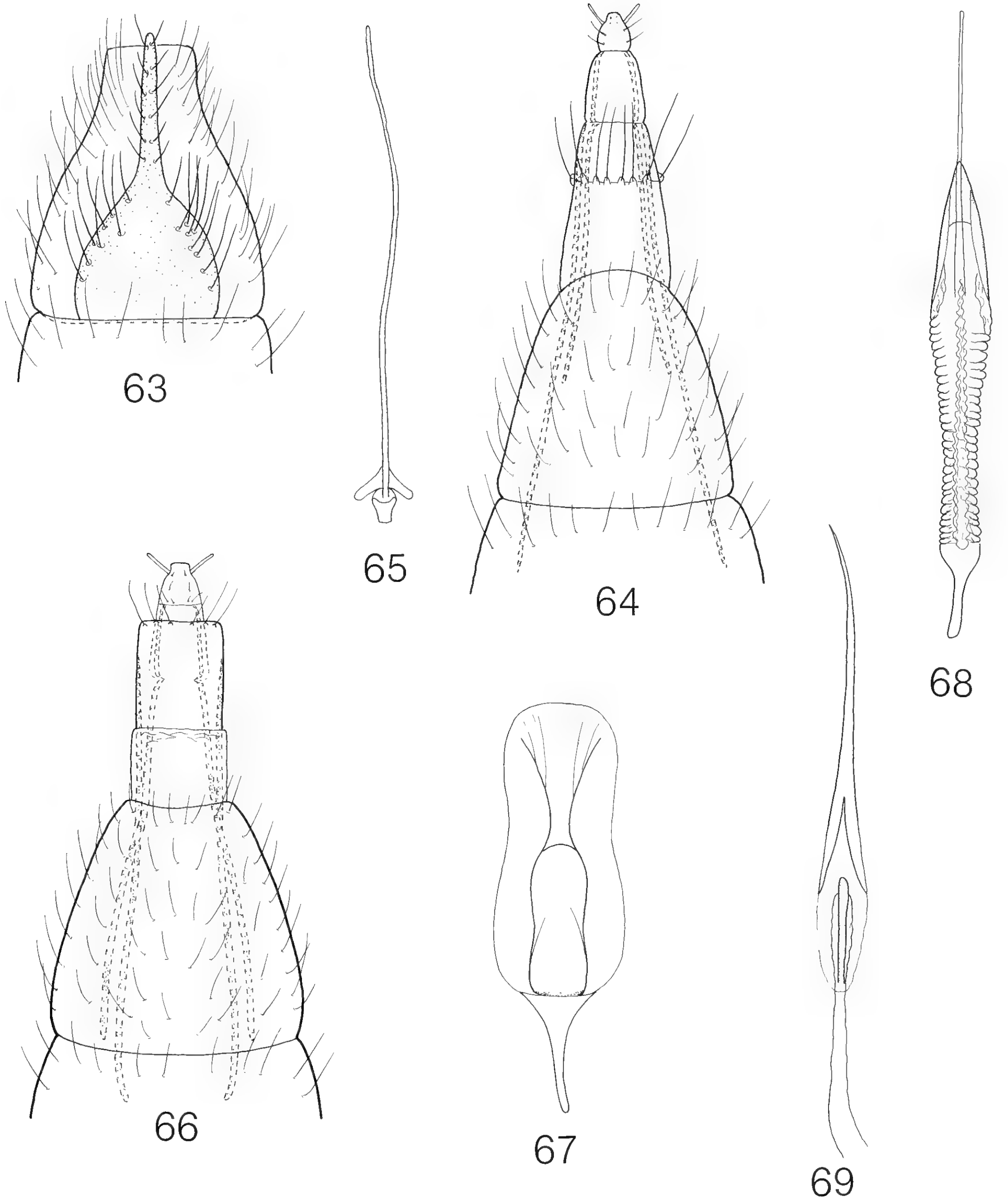
Male.—Length 1.6–18 mm. Brown in alcohol with no distinguishing patterns. Antenna with 18 segments, flagellum with segments of basal half slightly widened, scape greatly enlarged and setose. Abdominal segment VII annular, with bifid ventromesal process. Segment VIII tapering posteriorly in lateral view to acute apex; in ventral view square, apex with shallow mesal incision, posterolaterally with short horns. Segment IX short and fused with X dorsally, incomplete ventrally, lateral margins sclerotized; in lateral view appearing as linear process. Segment X truncate, shelf-like posteriorly, anteriorly produced into pair of slender apodemes extending through segment VIII; tergum thin, with mesal notch posteriorly. Phallus slender and elongate, wide basally and enclosed within a sheath posteriorly.

Female.—Unknown.

Type material.—Holotype, ♂: Panama, Barro Colorado Island, Snyder-Molino trail,



Figs. 53–62. Male genitalia. 53–57, *Alisotrichia asta.* 53, Lateral. 54, Dorsal. 55, Ventral. 56, Phallus, ventral. 57, Phallus, lateral. 58–62, *A. cuernita.* 58, Lateral. 59, Dorsal. 60, Ventral. 61, Phallus, ventral. 62, Phallus, lateral.



Figs. 63–69. Female terminalia. 63–65, *Alisotrichia kanukua.* 63, Abdominal segment VII, dorsal. 64, Abdominal segments, ventral. 65, Bursa copulatrix, ventral. 66–67, *A. neblina.* 66, Abdominal segments, ventral. 67, Bursa copulatrix, ventral. 68, *A. mathisi,* bursa copulatrix, ventral. 69, *A. paxilla,* bursa copulatrix, ventral.

marker 3, light trap I, 6–12 December 1989, H. Wolda. Paratypes: same data as holotype, but 13–19 December 1989, 1 ♂; same, but 21–27 December 1988, 1 ♂; same but light trap III, 13–19 December 1989, 1 ♂; same, but 10–16 January 1990, 1 ♂; same, but 30 January–5 February 1991, 1 ♂.

Etymology.—Spanish word for "little horn," referring to the distinctive processes from segment VIII.

Alisotrichia timouchela Botosaneanu

Alisotrichia timouchela Botosaneanu 1989: 98.

This species was described from two males collected in Martinique. We have a single male from Venezuela collected from a Malaise trap on the Rio La Viuda in the Parque Nacional Peninsula de Paria, Uquire. This is the same collection that yielded *A. viuda.*

ACKNOWLEDGMENTS

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TWO NEW GENERA TO ACCOMMODATE TWO NORTH AMERICAN PLANT BUGS (HETEROPTERA: MIRIDAE: PHYLINAE)

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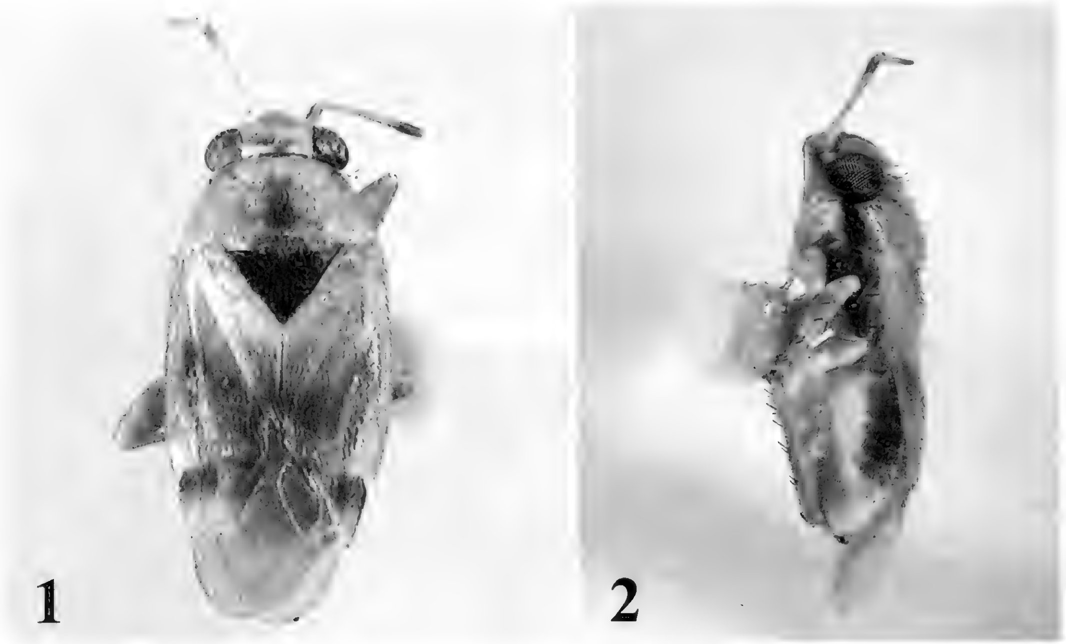
Abstract.—The new genus ***Sthenaropsidea*** is established to accommodate *Sthenarus mcateei* Knight, known from eastern United States, and the new genus ***Gonoporomiris*** is established for *Demarata mirifica* Distant, previously known from Veracruz, Mexico, and newly reported from Grand Bahama Island, the Dominican Republic, and Florida in the United States. Provided are illustrations of the male genitalia, adult dorsal and lateral photographs, new distribution records, and a discussion of relationships.

Key Words: Heteroptera, Miridae, *Sthenaropsidea, Gonoporomiris,* new genera, *Sthenarus mcateei, Demarata mirifica,* new combinations, Nearctic, distribution

In a continuing effort to clarify relationships among Nearctic Miridae, we have become aware that a number of North American species are not congeneric with the type species of their genera of current placement. One obvious example involves the placement of five North American species in the genus *Sthenarus* Fieber (Henry and Wheeler 1988, Schuh 1995). We have determined that none of the Nearctic species belong in *Sthenarus.* We are also are aware of problems involving the Palearctic species, including the possibility that even the type species, *Sthenarus rotermundi* (Scholtz), a species adventive in North America (Henry and Wheeler 1979, Wheeler and Henry 1992), may belong in another genus that has nomenclatural priority, thus, making *Sthenarus* a junior synonym. Because of this broader existing confusion and certain problems involving the North American taxa, it is not possible at this time to clarify the position of all Nearctic species now placed in *Sthenarus.* We are, however, able to determine that *S. mcateei* Knight, an unusual, vivid reddish-orange species is not congeneric with *Sthenarus,* nor does it belong in any other phyline genus we have studied.

Another long misplaced species is *Demarata mirifica* Distant (1893), described from Veracruz, Mexico, and known only from the holotype female. With the discovery of additional specimens of *D. mirifica* from the Grand Bahama Island, the Dominican Republic, and the United States, we are able to confirm the correct subfamily placement and determine that this species does not belong in any existing genus.

As a consequence, we establish the new genus *Sthenaropsidea* to accommodate *S. mcateei* and *Gonoporomiris* to accommodate *D. mirifica. Sthenaropsidea mcateei* and *G. mirifica* are redescribed, their distributions are summarized, and an adult dorsal habitus illustration of *S. mcateei,* figures of



Figs. 1–2. *Gonoporomiris mirificus* (♀) from Veracruz, Mexico. 1, Dorsal aspect. 2, Lateral aspect.

male genitalia, and dorsal and lateral photographs of both species are provided.

The following acronyms are used for institutions cited: AMNH (American Museum of Natural History, New York, NY); BNHM ([British] Natural History Museum, London); FSCA (Florida State Collection of Arthropods, Gainesville, FL); PU (Purdue University, West Lafayette, IN); UK (University of Kansas, Lawrence, KS); and USNM ([U.S.] National Museum of Natural History, Smithsonian Institution, Washington, DC).

Gonoporomiris Henry and Schuh, new genus

Type species: *Demarata mirifica* Distant 1873.

Diagnosis.—Phylinae: Phylini. Small, total length 2.36–2.84 mm, flattened dorsoventrally; antennal segment II weakly but distinctly clavate in both sexes. Genitalia with a rigid sclerotized vesica of the phyline type, vesica short and stout, secondary gonopore extremely large, occupying about one-half the length of vesica. Similar in appearance to certain species of *Rhinacloa,* but vestiture of dorsum composed only of recumbent simple setae, antennae not sexually dimorphic, and male genitalia distinctive because of the very large secondary gonopore.

Description.—Small, somewhat flattened; dorsum at most weakly shining, with vestiture of recumbent, short, golden, simple setae (Figs. 1–6). Head distinctly projecting beyond anterior margin of eyes in dorsal view; posterior margin more or less conforming to anterior margin of pronotum, posterior margin of vertex weakly carinate; head short dorsoventrally, eyes occupying nearly entire height of head in lateral view. Antennal segment II weakly clavate in both sexes. Claws of moderate length, curving, most strongly so on apical one-half; parempodia setiform, pulvilli large, extending nearly entire length of claw, adnate to claw over about one-half of length. Genitalia in male with short, stout, untwisted vesica; secondary gonopore very large, heavily spinose, occupying about one-half the length of vesica (Fig. 7); left paramere with a very long posterior process and short, blunt anterior process (Fig. 8); right paramere oval, greatly reduced (Fig. 9); phallotheca short, erect (Fig. 10).

Etymology.—Named for the extremely large secondary gonopore in the vesica of the male. Gender: masculine.

Discussion.—Although Carvalho (1952) synonymized *Demarata* Distant under the orthotyline genus *Ceratocapsus* Reuter, he did not make the formal combination of *C. mirificus* until later (Carvalho 1958). Schuh and Schwartz (1985) discussed the position of *D. mirifica* and concluded that it belonged in Phylinae, but were unable to determine the generic placement, given that the only known specimen was a female. More recently, Carvalho (1988) inexplicably argued that it belonged in the mirine genus *Dagbertus* Reuter, a position cataloged by Schuh (1995). Although the structure of the pretarsus would suggest placement in the Phylinae, it is only with knowledge of the male genitalia that this position now can be confirmed.

The genitalia of *Gonoporomiris* are distinctive because of the very large gonopore, which occupies about one half of the vesica (Fig. 7). The left paramere (Fig. 8), while having a form not unknown in the Phylinae, is nonetheless distinctive among New World taxa. They are additionally distinctive for the greatly reduced right paramere (Fig. 9).

Although *Demarata mirifica* has a resemblance to some species of *Rhinacloa* and possibly also to species of *Sthenaridea,* this similarity is apparently only superficial. The vesica is long, slender and twisted in all species of *Rhinacloa*; the gonopore is never strongly developed and not enlarged. Furthermore, *Rhinacloa* spp. also have a row of spicules distally on the dorsal surface of the hind femur, a feature which does not occur in *Gonoporomiris mirificus.* The vesica in *Sthenaridea* is always tubular and with the secondary gonopore in the form of a simple opening, rather than as what Schuh (1974) referred to as a "horse collar," a condition found on most Miridae. Furthermore, the structure of the parempodia in *Gonoporomiris* is setiform, whereas in *Sthenaridea* the parempodia are always strongly flattened and convergent.

Gonoporomiris mirificus (Distant),
new combination
(Figs. 1–10)

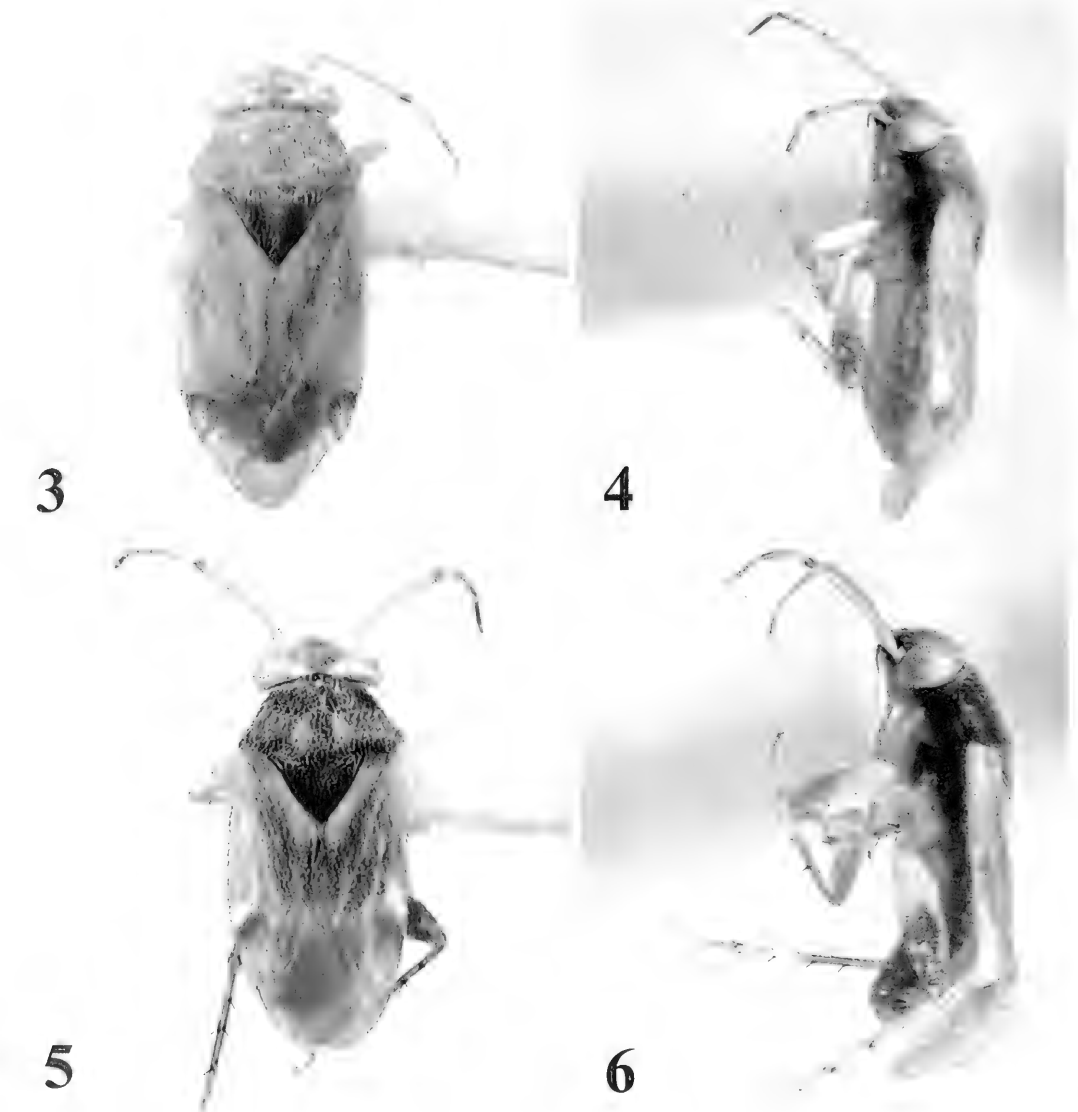
Demarata mirifica Distant 1893: 451 (n.sp.); Carvalho 1959: 355 (cat. as incertae sedis); Carvalho and Dolling 1976: 802 (disc. of type); Schuh and Schwartz 1985: 431 (disc. of generic and subfamily placement).

Ceratocapsus mirificus: Carvalho 1958: 47 (cat., n. comb.)

Dagbertus mirificus: Carvalho 1988: 100 (n. comb.); Schuh 1995: 752 (cat.).

Diagnosis.—Recognized by the small size, mean length of male 2.55 mm, the overall pale brown to reddish-brown coloration, weakly clavate antennal segment II in both sexes, simple golden setae on the dorsum, and the form of the male genitalia with the very large secondary gonopore. Dark males similar in appearance to *Rhinacloa forticornis* Reuter and paler females similar to *R. basalis* (Reuter) with head conforming to anterior margin of pronotum, but differ in the more reddish coloration, the head more strongly projecting beyond the anterior margin of the eyes, the weakly clavate antennal segment II in both sexes, the vestiture of only simple setae, and the distinctive form of the male genitalia with the short, stout vesica and very large secondary gonopore (Fig. 7), basally bulbous left paramere (Fig. 8), and greatly reduced right paramere (Fig. 9).

Description.—Small, brown, often tinged with red, although head, pronotum, and scutellum often darker than hemelytra, head pale along base and posteromesal margin of eyes. Antenna pale or white, except dark extreme distal portion of segment II. Membrane fumose, veins pale. Venter reddish to castaneous; metathoracic scent-gland eva-

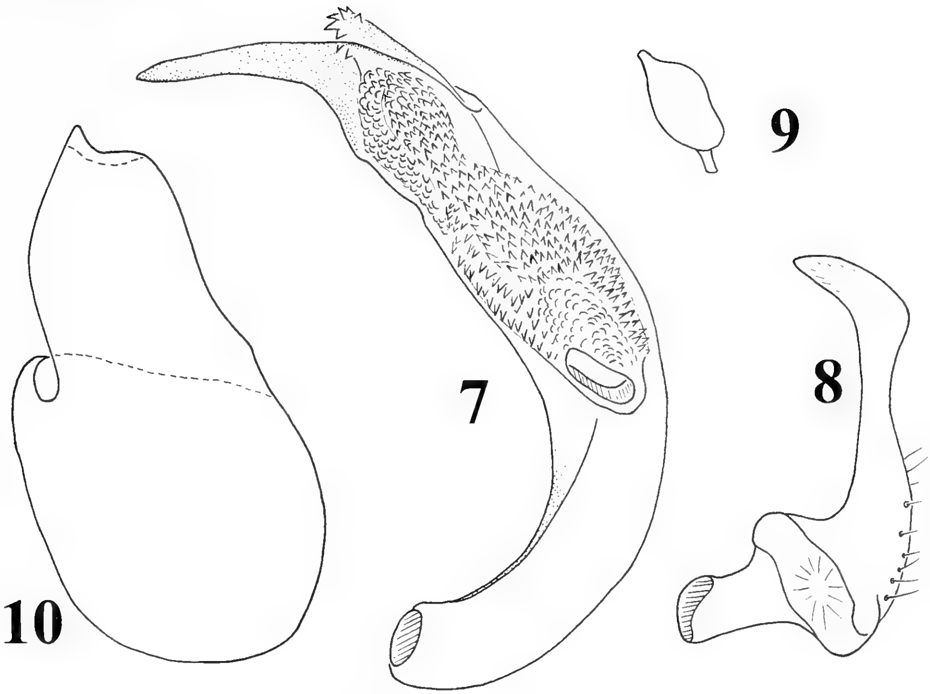


Figs. 3–6. *Gonoporomiris mirificus* from Grand Bahama Island. 3, ♂, dorsal aspect. 4, ♂, lateral aspect. 5, ♀, dorsal aspect. 6, ♀, lateral aspect.

poratory area pale. Legs, including coxae, mostly pale, metafemora often red to reddish brown on apical ⅓ to ½; tibial spines dark with pale bases. Male genitalia as in generic description (Figs. 7–10).

Male (n = 10): Length 2.36–2.61mm, width 0.91–1.06 mm. *Head:* Width 0.73–0.75 mm, vertex 0.32–0.36 mm. *Rostrum:* Length 0.99–1.04 mm, extending to apex of metacoxae. *Antenna:* Segment I, length 0.20–0.23 mm; II, 0.58–0.65 mm; III, 0.40–0.42 mm; IV, 0.31 mm. *Pronotum:* Length 0.40–0.46 mm, basal width 0.90–0.97 mm.

Female (n = 10; measurements of two Mexican females in brackets): Length 2.38–2.71 mm [2.76–2.84 mm], width 1.02–1.12 mm [1.20–ca. 1.28 mm]. *Head:* Width 0.73–0.77 mm [0.81–0.82 mm], vertex 0.33–0.35 mm [0.38–0.39]. *Rostrum:*



Figs. 7–10. Male genitalia of *Gonoporomiris mirificus*. 7, Vesica. 8, Left paramere. 9, Right paramere. 10, Phallotheca.

Length 0.99–1.04 mm [1.07 mm], extending to apex of metacoxae. *Antenna:* Segment I, length 0.17–0.20 mm [0.14–0.16 mm]; II, 0.50–0.59 mm [0.61–0.64 mm]; III, 0.42 mm [0.40 mm]; IV, missing [0.29 mm]. *Pronotum:* Length 0.42–0.46 mm [0.47–0.48 mm], basal width 0.91–1.00 mm [1.04–1.07 mm].

Host.—Unknown, except for one specimen below taken on a palm, *Copernicia* sp. Also, the large series from Grand Bahama Island was probably taken on the flowers of a cabbage palm, *Sabal* sp. (W. E. Steiner, pers. comm.).

Distribution.—Previously known only from Vera Cruz, Mexico, and now recorded from the Bahamas, the Dominican Republic, and the United States (Florida). The peculiar distribution of collection dates in the U.S. (dates 1929–1939, with one in 1908, one in 1957, 1 in 1975, 2 in 1991, 1 in 1996, and 1 in 2001) suggests that this species is adventive in Florida, perhaps becoming cyclically abundant or rare depending on periodic introductions. The lack of recent records could also indicate inadequate collecting, but one of us (TJH) collected extensively in the state during the 1980s and we have examined most collections containing Miridae from Florida and have found only six records since 1939.

We also note that the holotype female and other females from Mexico (Figs. 1, 2) and the Dominican Republic are slightly larger and lack the distinct reddish tinge typical of the material found on Grand Bahama Island (Figs. 3–6) and in Florida. However, the one associated male from the Dominican Republic compares well with males from the Bahamas and Florida, making us confident that all of this material is conspecific. Unfortunately, the Dominican Republic male is missing the abdomen and, thus, a positive confirmation is impossible. Clearly, more intensive surveys are needed to more fully determine the status of this enigmatic species.

Specimens examined.—DOMINICAN

REPUBLIC: 1 ♀, DISTRITO NACIONAL: Santo Domingo, Aug. 5, 1967, J. C. Schaffner, at black light (USNM); SANTIAGO: 1 ♂, Pedro Garcia, Aug. 23, 1967, J. C. Schaffner, at black light (USNM). GRAND BAHAMA ISLAND: 31 ♂, 33♀, Freeport, 20–27 June 1987, W. E. Steiner, M. J. & R. Molineaux (4 ♂, 4 ♀ AMNH; USNM). MEXICO: VERACRUZ: Holotype ♀, Atoyac, May, H. H. Smith (BNHM); 2 ♀, Cordoba, 14–15 Apr. 1908, F. K. Knab (USNM). USA: FLORIDA: 1 ♀, *Alachua Co.,* 10-10-29, A. M. Towles (USNM); 2 ♂, *Alachua Co.,* 1-IX-91, D. H. Habeck, at blacklight (FSCU); 1 ♀, *Brevard Co.,* Indian River, 1-13-30, J. R. Barass (USNM); 2 ♂, 1 ♀ [no specific locality], 1-13–18-30, J. R. Barass (1 AMNH, 2 USNM); 3 ♂, *Dade Co.,* Coconut Grove, 8-9-30, R. H. Beamer (UK); 1 ♂, *Dade Co.,* 3475 Main Highway, 24–25 July 1996, J. Brambilia, at blacklight (FSCA); 1 ♂, *Dade Co.,* Montgomery Botanical Center, 11901 Old Cutler Rd, 21 Feb. 2001, T. Dobbs, on *Copernicia* sp. (FSCA); 2 ♂, 1♀, *Handry Co.,* LaBelle, July 16, 1939, R. H. Beamer, P. Oman (UK, USNM); 1 ♂, *Flagler Co.,* 2-28-29, D. B. Webb (USNM); 1♂, 1 ♀, *Hillsboro Co.,* 2-8–15-30, B. P. Moora (USNM); 1 ♀, *Lee Co.,* Estero, May 6–12, 1908, E. P. Van Duzee (CAS); 1 ♀, Ft. Myers, 8-11-30, J. Nottingham (UK); 1 ♀, Ft. Myers, September 18, 1957, J. P. Kramer (USNM); 2 ♀, *Marion Co.,* 1-27-30, A. M. Towles (AMNH, USNM); 2 ♀ [no specific locality], 1-27-30, A. M. Towles (USNM); 1 ♂, *Putnam Co.:* no specific locality, January 7, 1930, A. M. Townes (AMNH); 1 ♂, *St. Lucie Co.:* Ft. Pierce, 8-7-30, P. W. Oman (UK).

Sthenaropsidea Henry and Schuh, new genus

Type species: *Sthenarus mcateei* Knight 1927.

Diagnosis.—Phylinae: Phylini. Small, total length 2.88–3.00 mm, delicate, broadly rounded; body color bright reddish orange, appendages pallid to white; hemelytra finely punctate, becoming translucent on clavus and corium, especially along inner half; legs slender, length of metatibial spines two or more times diameter of segment, all tibial spines pale, lacking dark basal spots; vesica strongly twisted, with three slender, acute, apical spiculi, dorsal edge with a coarsely toothed keel or carina, subapical secondary gonopore large and distinct.

Description.—Delicate, broadly rounded, shiny, width of hemelytra nearly equal to ½ of total length (Figs. 11–13); overall pubescence simple, semierect. Head broader than long, vertex in males subequal to combined dorsal widths of eyes, width of vertex in female ca 2.5 times combined dorsal widths of eyes; eyes lacking microsetae, occupying ¾ or more lateral height of head, deeply emarginate to accommodate antennal fossae on ventral half of anterior aspect. Antenna slender, segment I shortest, stoutest, apical diameter subequal to diameter of protibia, segment II longest, diameter subequal to basal diameter of protibia. Pronotum trapeziform, shiny, impunctate, basal width slightly greater than 2 times median length, anterior angles broadly rounded, basal margin straight or truncate. Mesoscutum broadly exposed, impunctate. Scutellum equilateral, impunctate. Hemelytron broadly rounded, finely punctate, corium and apical half of clavus translucent, pubescence simple, relatively long, semierect; apical ⅓ of cuneal fracture often curved downward; membrane mostly translucent, transparent at base and inside of areoles, veins forming two distinct areoles. Ventral surface shiny, with only semierect simple pubescence. Legs slender, unmarked, tibial spines concolorous with segments, always lacking basal spots; metatibial spines long, length 2 or more times diameter of segment; tarsi slender, segment III longest; claws slender, broadly rounded, parempodia setiform, pulvilli absent or greatly reduced. Male genitalia: Genital capsule smooth, simple, without ridges or tubercles; vesica (Fig. 14) stout, strongly spiraled, with 3 slender,

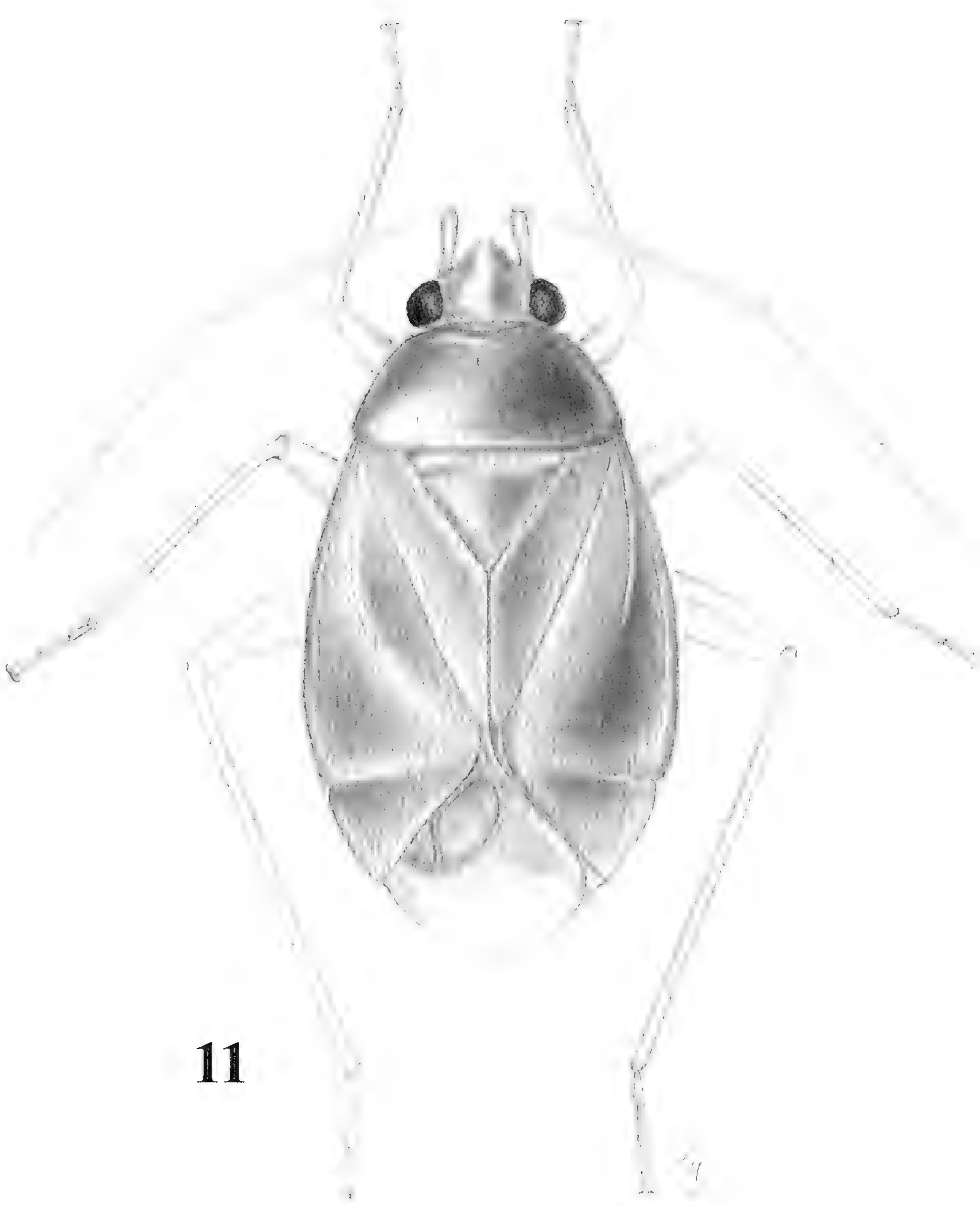
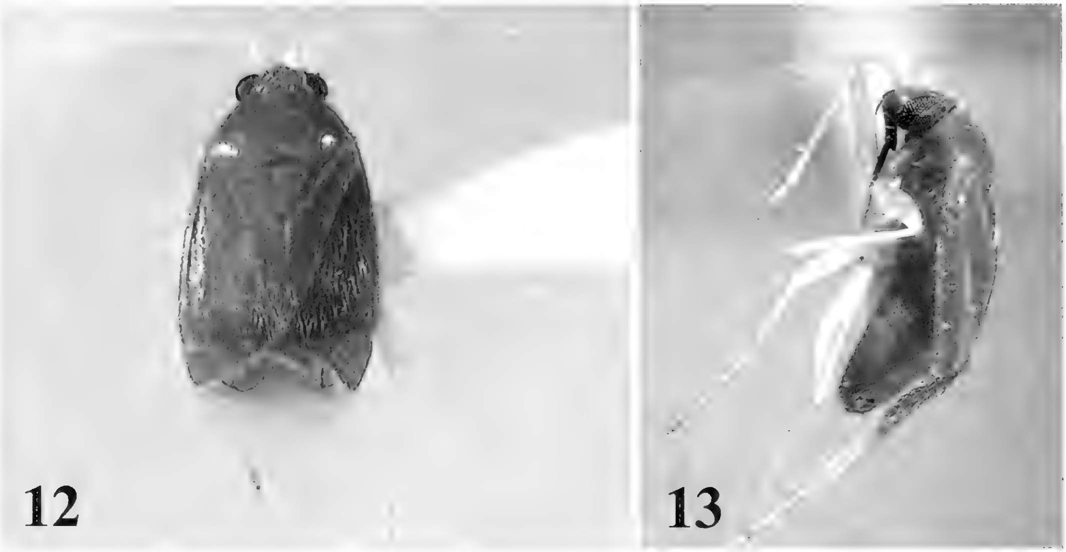


Fig. 11. Dorsal aspect of *Sthenaropsidea mcateei* (♀).

acute, apical spiculi, dorsal edge of apical ⅓ with a bluntly serrated keel or carina; secondary gonopore large; left paramere (Fig. 15) with posterior process about 2× longer than anterior process; right paramere (Fig. 16) elongate oval; phallotheca (Fig. 17) elongate, apically acute.

Etymology.—The generic name, taken from the prefix of the generic name *Sthenarus,* and from the Latin "idea," to indicate



Figs. 12, 13. *Sthenaropsidea mcateei* (♂). 12, Dorsal aspect. 13, Lateral aspect.

the historical but not phylogenetic association of *Sthenaropsidea.* Gender: feminine.

Discussion.—The male genitalia of *S. mcateei* are unique in the Phylinae because of the stout, strongly spiraled vesica having an irregular raised ridge on the dorsal edge of apical ⅓ (Fig. 14). Furthermore, *S. mcateei* is unlike any other known phyline in having a bright reddish-orange, broadly rounded body, strongly contrasted by the delicate pale or white antennae and legs.

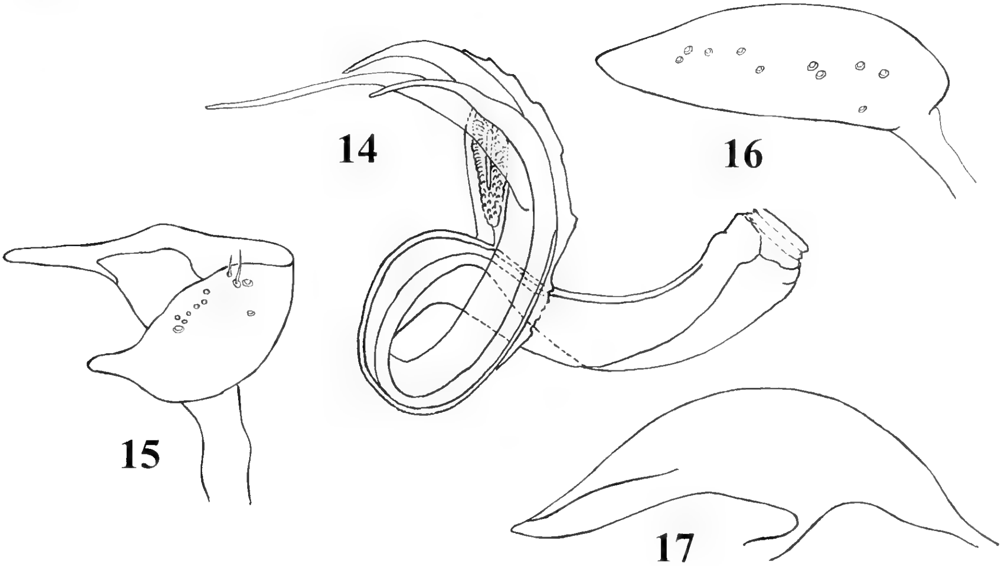
Sthenaropsidea mcateei (Knight), **new combination**
(Figs. 11–17)

Sthenarus mcateei Knight 1927: 9 (n.sp.); Snodgrass et al. 1984: 852 (list, host); Henry and Wheeler 1988: 500 (cat.); Schuh 1995: 434 (cat.)

Diagnosis.—Distinguished from all other North American Phylinae by the broadly rounded, delicate, bright reddish-orange body (Figs. 6–8), the pallid to white legs and antennae, and the unique twisted male vesica.

Description.—Body coloration shiny reddish orange, dorsum clothed with long, semierect, simple, pale setae. Head and pronotum shiny reddish orange, impunctate, calli weakly developed, not or only vaguely raised; rostral segment I and basal half of II dark reddish brown, segments III and IV pallid or pale yellowish brown. Mesoscutum and scutellum shiny reddish orange, impunctate, scutellum weakly transversely rugose. Hemelytron sparsely and finely punctate, thickly set with long, semierect pale yellow setae, uniformly shiny reddish orange, clavus and inner ½ of corium and paracuneus becoming translucent, pale, yellowish brown, membrane translucent yellowish brown, usually more transparent along cuneal margin and inside of areoles, veins reddish orange. Ventral surface uniformly shiny reddish orange, abdomen often becoming more yellowish brown ventrally. Ostiolar peritreme pale or white. Legs uniformly pallid to almost white, including tibial spines; claws pale yellow brown. Male genitalia: Vesica (Fig. 14); left paramere (Fig. 15); right paramere (Fig. 16); phallotheca (Fig. 17).

Male (n = 5): Length: 2.88–3.00 mm, width 1.35–1.40 mm. *Head:* Width 0.64–0.66 mm, width of vertex between eyes 0.30 mm. *Antenna:* Segment I, length 0.24



Figs. 14–17. Male genitalia of *Sthenaropsidea mcateei*. 14, Vesica. 15, Left paramere. 16, Right paramere. 17, Phallotheca.

mm; II, 1.14–1.18 mm; III, 0.64–0.78 mm; IV, 0.42–0.52 mm. *Rostrum:* Length 1.28–1.30 mm, extending beyond coxae to 4th or 5th abdominal segment, nearly to base of genital capsule. *Pronotum:* Length 0.46–0.48 mm, basal width 1.02–1.04 mm.

Female (n = 9): Length 2.59–2.92 mm, width 1.36–144 mm. *Head:* Width 0.61–0.62 mm, width of vertex between eyes 0.36–0.37 mm. *Antenna:* Segment I, length 0.22–0.24 mm; II, 1.04–1.07 mm; III, 0.54–0.59 mm; IV, 0.42–0.44 mm. *Rostrum:* Length 1.30–1.31 mm, extending to base of ovipositor. *Pronotum:* Length 0.46–0.48 mm, basal width 1.02–1.08 mm.

Hosts.—*Sthenaropsidea mcateei* specializes on members of the grape family Vitaceae. The type series from Odenton, Maryland, was taken on wild grapevine, *Vitus* sp. (Knight 1927); adults and nymphs were collected by TJH and A. G. Wheeler, Jr. on wild grape (*Vitis* sp.) in Arkansas; and Snodgrass et al. (1984) found this species in Mississippi on pigeon grape (*Vitis cinerea* Engelm.), peppervine (*Ampelopsis arborea* (L.) Koehne), another vitaceous vine), and *Cornus drummondi* C. A. Meyer. Their (Snodgrass et al. 1984) record from *Cornus* undoubtedly represents an accidental record or a case of the trees having a vitaceous vine growing among them.

Distribution.—Previously recorded from Maryland and Mississippi (Henry and Wheeler 1988, Schuh 1995). Arkansas, Indiana, and Louisiana are new state records.

Specimens examined.—USA: ARKANSAS: 1 ♀, *Clark Co.,* Arkadelphia, Ouachita Bap. Univ., 10 June 1987, T. J. Henry and A. G. Wheeler, Jr., taken on *Vitis* sp. (USNM); 1 ♀, *Clark Co.,* Rt. 8, 1 mi. SE Griffithtown, 10 June 1987, T. J. Henry and A. G. Wheeler, Jr., taken on *Vitis* sp. (USNM). INDIANA: 1 ♀, *Tippecanoe Co.,* 7 July 1939, D. W. LaHue, light trap (PU). LOUISIANA: 3 ♂, 2 ♀, *Natchitoch Parish,* Kisatchie Natl. For., 18 June 1988, at MV & blacklight, D. A. Rider (D. A. Rider colln., Fargo, ND; 1 ♂ USNM). MARYLAND: Holotype ♀ (29 July 1917 and 4 paratype ♀ (12 July 1914), Odenton, on *Vitis,* W. L. McAtee coll. (USNM); 2 ♂, 1 ♀, *Prince Georges Co.,* Cheverly, 38°56′N 76°55′W, 9 July 1992, W. E. Steiner and J. M. Swearingen (USNM; 1 ♂ AMNH).

MISSISSIPPI: 1 ♂, 3 ♀, *Washington Co.*, Stoneville, 29 June 1982, G. L. Snodgrass coll., taken on *Ampelopsis arborea, Cornus drummondi,* and *Vitis cinerea* (1 ♀ AMNH; USNM).

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THE NEW WORLD GENUS *CYCLONEDA* CROTCH (COLEOPTERA: COCCINELLIDAE: COCCINELLINI): HISTORICAL REVIEW, NEW DIAGNOSIS, NEW GENERIC AND SPECIFIC SYNONYMS, AND AN IMPROVED KEY TO NORTH AMERICAN SPECIES

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Abstract.—Taxonomic, nomenclatoral, and comparative morphological studies of *Cycloneda* Crotch are reviewed. The genus is diagnosed and compared to both related and superficially similar taxa. *Pseudadonia* Timberlake is recognized as a junior synonym (**n. syn.**). The species composition of the fauna is delineated, but the need to re-examine species limits and nomenclatoral priorities is stressed. New synonyms are proposed for two species of *Cycloneda* occurring in North America: *Coccinella krikkeni* Iablokoff-Khnzorian, reported from India, and *Cycloneda atra* Casey (of unknown origin) are **new junior synonyms** of *Cycloneda munda* (Say); *Cycloneda hondurasica* Casey (Honduras) and *Coccinella reflexa* Germain (Chile) are **new junior synonyms** of *Cycloneda sanguinea* (Linnaeus). *Adalia galapagoensis* Van Dyke is transferred to the genus *Cycloneda* (*Cycloneda galapagoensis*, **n. comb.**) and identified as a close relative of *Cycloneda sanguinea. Cycloneda sanguinea caymana* Chapin is elevated to full species status (*Cycloneda caymana,* **n. status**). A new key to species of North American *Cycloneda* is provided.

Key Words: *Cycloneda, Coccinellina, Pseudadonia,* Synonychini, Coccinellini, lady beetle, systematics, synonymy, Nearctic, Neotropical

Cycloneda Crotch is a New World genus of lady beetles in the tribe Coccinellini. In Central and South America (Blackwelder 1945), the genus is a composite one, comprising an assemblage of two dozen or more species which generally share a rounded convex body form, highly polished cuticle, and little else. In contrast, the three North America indigenes—*Cycloneda sanguinea* (L.) (type species), *C. munda* (Say), and *C. polita* Casey—appear to form a close-knit, monophyletic group, whose members often have been confused in the literature (Gordon and Vandenberg 1993). These species are characterized by red to yellowish elytra without black spots, and a black pronotum with a white border design and pair of discal spots (Fig. 9). The basic components of the white design are often coalesced to form a complete or broken ring in each lateral third (Figs. 2, 5), and a median spur shaped mark is often present at anterior border (Figs. 2, 5, 8).

The North American *Cycloneda* were keyed and diagnosed most recently by Gordon (1985), who followed Leng (1903) in the use of pronotal color patterns and elytral ground color in the separation of species (treated as varieties by Leng 1903). Unfortunately, these selected attributes are less than completely reliable, particularly in the identification of specimens from the western United States. In addition, both of the above authors excluded the species *Cycloneda atra* Casey (1899) from their revisions on the assumption that the unique all-black type specimen from an unrecorded locality was unlikely to be a member of the North American fauna.

Here, I resolve the identity of *Cycloneda atra* and that of a second equally mysterious specimen from Southern India described by Iablokoff-Khnzorian (1982) as *Coccinella krikkeni* Iablokoff-Khnzorian. The identities of *Coccinella reflexa* Germain (1854) from Chile and *Cycloneda hondurasica* Casey from Central America also are investigated. As a result, four new synonyms are proposed, two each for *Cycloneda munda* and *Cycloneda sanguinea.* The taxonomic history of the genus *Cycloneda* is reviewed, the composition of the Neotropical *Cycloneda* fauna discussed, and a new key to North American *Cycloneda* is proposed to make the identification of species more reliable.

HISTORICAL RESUMÉ

The name *Cycloneda* was first applied by Crotch (1871) as a replacement name for *Daulis* Mulsant (1850) (preoccupied by *Daulis,* Erichson 1842). Although Crotch had restricted use of the name to the New World fauna (about 40 species), he still refered to *Cycloneda* as "an unsatisfactory assemblage of species having but little in common" and lamented the lack of characters to separate it into meaningful groups (Crotch 1874). The subsequent designation of *Coccinella sanguinea* Linnaeus as the type species of *Cycloneda* (Crotch 1874) only added to existing taxonomic confusion. While *C. sanguinea* clearly exemplified the rounded convex body form (Figs. 8, 10) of most of its nominal congeners, it was not particularly closely related to the majority of them. Conversely, many of its true affiliates (Figs. 12, 13) were relegated to other genera because of their flatter, more elongated forms. Subsequent authors provided keys and diagnoses for *Cycloneda* (Casey 1899, Leng 1920), but clearly concerned themselves only with an easily definable subgroup consisting of the three North American species (*C. sanguinea, C. munda, C. polita*) and synonyms thereof. Casey split off two new genera—*Olla* (1899) and *Spiloneda* (1908)—but this did little to improve the overall classification. With the transfer of additional species to *Olla* (Casey 1908), that genus soon proved as heterogeneous and ill-defined as *Cycloneda* (Vandenberg 1992). *Spiloneda,* on the other hand, has remained monotypic because it was stipulated for "such forms as Gilardini, Muls., from Colombia and Central America . . ." (Casey 1908) without detailing additional species names or distinguishing traits.

The examination of internal genital structures was an important advancement for lady beetle taxonomy, although it conferred no immediate benefit to the classification of *Cycloneda* species. Weise introduced the use of male genitalia (shape of basal lobe) for distinguishing lady beetles of similar habitus (e.g., Weise 1904b), but did not use these structures for defining genera or determining broader relationships. He contributed a heterogeneous assortment of new species to *Cycloneda* between 1898 and 1922 (Weise 1898, 1902, 1904a, 1906, 1922).

Wilson (1926) conducted a morphological study on the male and female genitalia of selected representatives of the family Coccinellidae. He found characteristics which suggested a close relationship between *Cycloneda* and *Coccinella,* and indicated that the male genitalia of *Olla* were so extraordinary as to set it well apart from the other genera studied. Wilson's observations appear to have been overlooked by a subsequent generation of lady beetle taxonomists who continued to stipulate minor differences in external morphology, while ignoring the abundant generic characters provided by genital structures.

Chapin (1941) was one of the first specialists to question the value of external characteristics used to separate *Cycloneda* from the Neotropical genera *Neda* Mulsant, *Procula* Mulsant, and *Olla,* all of which had been grouped together in the tribe Synonychini. He found that ranking a random selection of 17 species by epipleural width or depth of mesosternal emargination (at the time considered key differentiating characteristics), failed to segregate species according to their presumed generic placement or to produce significant breaks between groups of species in the series. In contrast, he observed that three or more definite types of genitalia could be found within the series, yet he made no attempt to revise generic assignments based on that observation.

Timberlake (1943) refined the definition of *Cycloneda* by restricting the name to "*sanguinea* and allies with immaculate elytra." He described three new genera for some of the former *Cycloneda* species based on material in the famous Koebele Collection—*Paraneda, Erythroneda,* and *Chloroneda.* Unfortunately, he did not study types or material from South America which might have allowed him to resolve some of the erroneous species synonymies proposed by Crotch (1874) and perpetuated by other authors. He was uncertain, therefore, of the number of valid species which should have been included in each of these new genera.

Timberlake (1943) also described the genus *Coccinellina* (type species *Coccinella emarginata* Mulsant) (Fig. 13) for Neotropical species formerly classified in *Coccinella,* and the genus *Pseudadonia* (type species *Pseudadonia chiliana* Timberlake) (Fig. 12) based on a single male specimen from Chile with dilated front and middle basitarsi (compare Figs. 15 and 16). Timberlake's generic key characterized the epipleura of *Coccinellina* and *Pseudadonia* species as "horizontal and never much expanded" and those of *Cycloneda* species as "more or less inclined and descending externally or very broad."

Despite an often noted resemblance between *Cycloneda* species (sensu Timberlake 1943) and *C. emarginata* (Mulsant 1850, Crotch 1874, Koebele *in* Timberlake 1943), Timberlake did not make a rigorous comparison between *Cycloneda* and his new genus *Coccinellina,* undoubtedly influenced by the fact that members of these genera conventionally were placed in two distinct tribes (Synonychini and Coccinellini, respectively) (Korchefsky 1932). Actually, both nominal genera exhibit a wide range of epipleural architecture with considerable cross-generic overlap. Although *Cycloneda sanguinea* (type) may be said to have broad epipleura which are steeply inclined externally (Fig. 7), its congeners, *C. polita* (Fig. 4) and *C. munda,* (Fig. 1) have narrower epipleura which are nearly horizontal, as in *Coccinellina emarginata.* The epipleura of *C. pulchella* (placed in *Coccinellina* by Timberlake) (Fig. 14) are broader than in either *Cycloneda polita* or *C. munda.* There is also significant sexual dimorphism: in all of the aforementioned species, the male epipleura tend to be broader and more steeply inclined than the female epipleura.

Mader (1958) provided a key to *Cycloneda* species and former *Cycloneda* species useful for identification purposes, but based almost entirely on color patterns. He made no attempt to validate or refute the genera proposed by Casey and Timberlake, and did not discuss male genital characters.

Chapin (1969) synonymized *Pseudadonia chiliana* with *Coccinella fulvipennis* (placed in *Coccinellina* by Timberlake). Chapin continued to recognize *Pseudadonia* as a valid genus even though the distinctive characteristic of the inflated basitarsi of the type specimen was confirmed as gender specific, and no derived characteristic was identified for *Coccinellina* which would exclude *C. fulvipennis* from membership.

Several important regional works covering the genus *Cycloneda* were published in the next two decades. Gordon (1985) revised the North American *Cycloneda* species, but did not attempt to review non-North American species names and types for possible synonymies. Gordon compared the external morphologies of *Cycloneda* and *Olla* and contrasted the male and female genitalia, but recognized the need to study the Neotropical species in order to assess the significance of observed differences and determine generic boundaries. Iablokoff-Khnzorian (1982) included some remarks on New World Coccinellidae in his revision of the Old World species. He concluded that *Cycloneda* is most closely related to *Harmonia* and *Xanthadalia,* but he classified a newly discovered species (*C. krikkeni* Iablokoff-Khnzorian) with a remarkable resemblance to *Cycloneda munda* in the genus *Coccinella.*

Arioli (1985) contributed an analysis (similarity phenogram) of the Coccinellini of Rio Grande do Sul, Brasil. She utilized some characters with good potential as indicators of phylogenetic relationships (e.g., male genitalia, postmetacoxal line, pronotal maculation), but the addition of too many trivial (labile) characters (e.g., coloration of certain structures) had the effect of obscuring some of the relationships otherwise nicely revealed in her analysis, and in one case yielded the lowest similarity coefficient for a male and female of the same species.

The idea of synonymizing *Coccinellina* with *Cycloneda* was first suggested publicly by Iablokoff-Khnzorian in an informal correspondence to *Coccinella* newsletter (1990), although it was proposed earlier in a format not intended as a permanent scientific record (Vandenberg 1987). Vandenberg published a series of papers between 1988 and 1996 which refined and clarified the relationships between *Cycloneda* and other taxa, but which focused primarily on the revision (*Erythroneda, Olla*) or new description (*Cirocolla* Vandenberg, *Spilindolla* Vandenberg) of genera whose species had been improperly classified in *Cycloneda.* The close relationship between *Cycloneda* and three other genera—*Coccinella, Erythroneda,* and *Neocalvia*—was briefly discussed in a revision of the genus *Erythroneda* (Vandenberg and Gordon 1988). Vandenberg (1992) revised the genus *Olla,* provided a key to major genitalic archetypes occurring in the former Synonychini and indicated the proper genus group affiliation for each genitalic configuration. These different archetypes undoubtedly correspond to the several categories referred to by Chapin (1941) in his studies of the male genitalia of *Cycloneda* sensu lato. Although Chapin's work did not list the species examined, his handwritten records and slide collection at the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), show that he dissected examples of each of the disparate lineages classified in *Cycloneda* at that time. Vandenberg's treatment of the new genus *Spilindolla* (Vandenberg and Gordon 1996) provided additional information and genitalic illustrations for separating Neotropical lady beetle genera and generic groups. Using these improved criteria to determine relationships, the male and female genitalia of most "*Cycloneda*" species segregate with *Neda, Olla, Spiloneda, Paraneda,* and allied genera, or with *Egleis* Mulsant and allies, while those of the type species and a minority of others reveal a much closer relationship to *Coccinella.* Vandenberg (1992) also indicated differences between the larval dorsal armature of *Cycloneda* and superficially similar species allied to *Olla,* and, in a later work (Gordon and Vandenberg 1993), identified distinctive features of the larval head capsule and microsculpturing for separating species of *Olla, Cycloneda,* and *Coccinella.*

Thus, *Cycloneda* has been a composite genus since its conception in 1871. A few species have been removed through the creation of new genera, but taxonomic progress has been hindered severely by 1) the nearly exclusive use of superficial and poorly defined external characters to determine generic assignments, 2) failure either to examine the male and female genitalia or to attach proper evolutionary significance to their observed patterns of similarity, 3) a tendency for researchers to focus on taxa from only one region, one tribe or a single collection, and 4) the description of new species based on unknown (*Cycloneda atra*) or dubious (*Coccinella krikkeni*) type localities, which were then omitted from later regional studies.

The genus *Cycloneda* (as recognized here) is in need of a complete species level revision. Many species exhibit both clinal variation (Vandenberg 1997) and discrete polymorphism; others appear poorly differentiated from their congeners, making the delimitation of the different species particularly challenging. I hope that the present preliminary contribution will be of use to those who wish to pursue this interesting area of investigation.

Genus *Cycloneda* Crotch

Cycloneda Crotch 1871: 6 (list of species) (Type species: *Coccinella sanguinea* L., by subsequent designation of Crotch 1874); 1873a: 371 (U.S. revision); 1873b: 50 (N. Amer. checklist) 1874: 162 (world revision); Gorham 1892: 169 (C. Amer., distribution); Casey 1899: 84 (U.S., generic key); 1908: 404 (generic limits); Leng 1920: 216 (N. Amer. catalog); Wilson 1926: 63 (genital morphology, generic comparisons, higher classification); Korschefsky 1932: 282 (world catalog); Chapin 1941: 165 (generic comparisons); Timberlake 1943: 23 (generic limits); Wingo 1952: 24 (Mex., C. and S. Amer., W. Indies checklist); Mader 1958: 238 (Amer. key to species); Hatch 1961: 181 (N. Amer. generic key); J.Chapin 1974: 62 (Louisiana revision); Belicek 1976: 330 (W. Can., Alaskan revision); Gordon 1985: 819 (N. Amer. revision, prey, distributions, genitalia); Vandenberg and Gordon 1988: 33 (generic comparison); Iablokoff-Khnzorian 1990: 460 (diagnosis, generic comparison); Vandenberg 1992: 372 (higher classification); Gordon and Vandenberg 1993: 302 (larval descriptions, N. Amer. larval key, larval generic comparisons); Vandenberg and Gordon 1996: 547 (generic comparisons); Vandenberg 1997 (example of clinal variation in *C. ancoralis*).

Neda (*Cycloneda*): Chapuis 1876: 201.

Daulis Mulsant 1850: 296 (Type species: not designated) (not *Daulis* Erichson 1842); Crotch 1874: 162 (as synonym of *Cycloneda*) (world revision); Berg 1874: 290; Chapuis 1876: 201 (as synonym of *Neda* (*Cycloneda*) (diagnosis).

Coccinella (*Cycloneda*) Leng 1903: 202 (N. Amer. key).

Coccinellina Timberlake 1943: 15 (Type species: *Coccinella emarginata* Mulsant): Iablokoff-Khnzorian 1990: 59 (as synonym of *Cycloneda*).

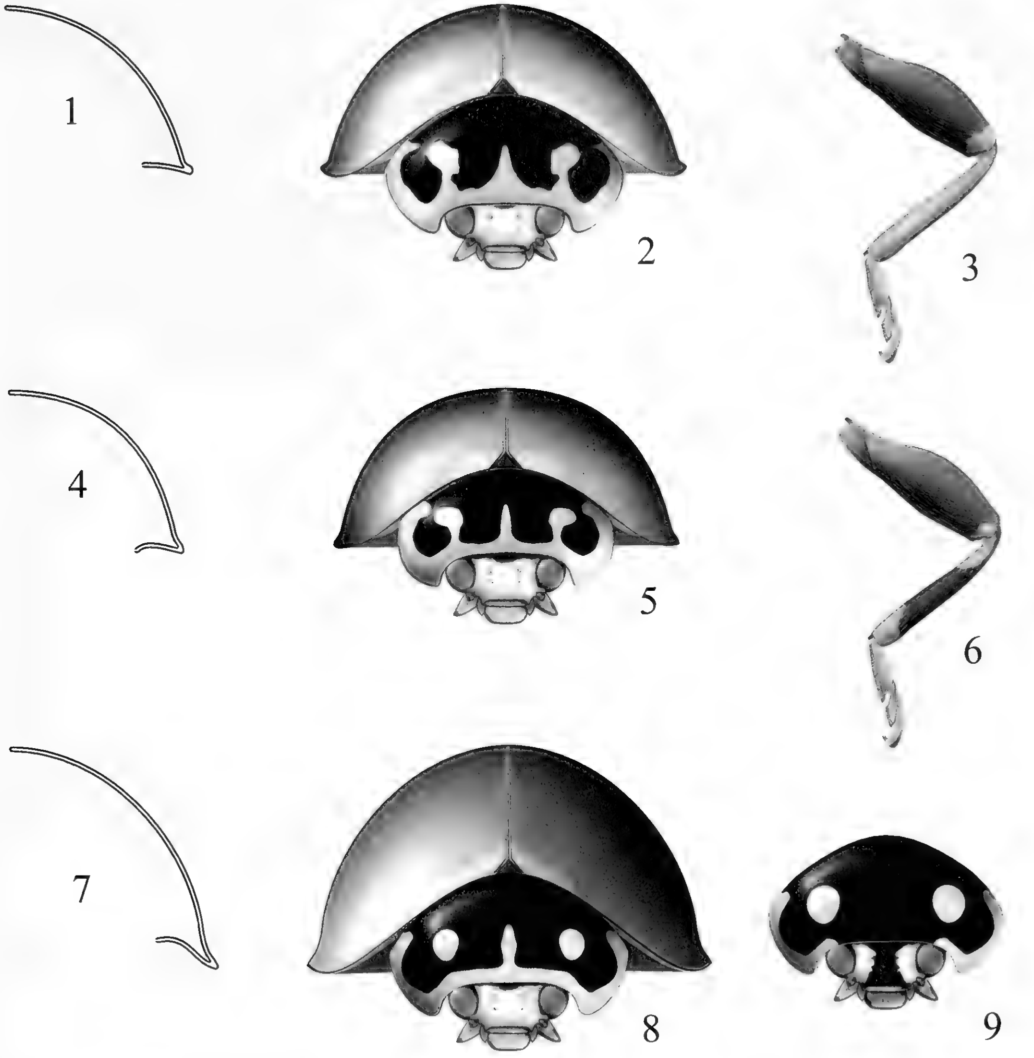
Pseudadonia Timberlake 1943: 53 (Type species: *Pseudadonia chiliana* Timberlake) (preoccupied name, not *Pseudadonia* Handlirsch 1906); Chapin 1969: 468. **New synonym.**

Diagnosis.—Distinguished from most other genera by the characteristic repertoire of pronotal color patterns which vary as shown (Figs. 2, 5, 8, 9, 10, 11, 12, 13, 14), or derive from Figs. 8 and 9 through loss of discal spots, or from Figs. 2 and 5 through extension of pale areas to form complete ring or solid white oval in each lateral third; head with gender specific color patterns as shown (Figs. 8, 9), ranging to all or mostly white in males and all or mostly black in females; elytra deep red to flavous or rarely ashen, with or without additional black and or white marks; venter black to dark brown marked with lighter patches. Postmetacoxal line incomplete, closely paralleling hind margin of first abdominal sternite in outer third; oblique line obsolete or represented by faint to moderately distinct integumental wrinkle (as opposed to a sharply incised line). Middle and hind tibiae with pair of spurs at apex. Infundibulum of female genitalia (Fig. 25) well developed, flared at distal end and often bearing a bulblike enlargement (sometimes obscure due to transparency) at proximal (bursal) end; sipho of male genitalia (Fig. 23) constricted before apex, terminating in a membranous area with imbedded spicules (reduced in some species); siphonal capsule well developed, often pigmented, with inner arm arcuate to angulate, outer arm often crested externally; basal lobe (Fig. 24) undivided; basal piece never highly elongated, more or less quadrate; parameres well separated at base.

Remarks.—Lady beetles with similar pronotal color patterns occur occasionally in other coccinelline genera. Species of *Adalia* with a very similar appearance can be distinguished by the form of the postmetacoxal line which recurves toward the abdominal base. *Olla* and allied genera, which make up the bulk of the Neotropical coccinelline fauna (*Olla, Cirocolla, Spilindolla, Spiloneda, Neda, Mononeda* Crotch, *Neoharmonia* Crotch, *Procula, Paraneda, Clynis* Mulsant, *Chloroneda*), depart radically from *Cycloneda* in the form of the genitalia of both sexes: female with infundibulum absent or rarely present as a simple tubular and weakly sclerotized sheath; sipho of male genitalia not constricted before apex, terminating in a simple rounded opening, preapical projections or lobes often present; basal lobe often divided (Figs. 20–22); basal piece generally longer than wide, often highly elongate. Species related to *Mulsantina* Weise and *Egleis* can be separated by the absence of tibial spurs as well as by the form of the male (Fig. 19) and female genitalia (see Vandenberg 1992, Vandenberg and Gordon 1996 for further details).

Genera related to *Cycloneda* share the same major genitalic features outlined in the diagnosis above. Most of these can be separated easily by more obvious external characters. *Cycloneda* differs from the related genera *Erythroneda* and *Neocalvia* by the presence of black to very dark brown pigmentation on the head, pronotum and venter; the latter two genera also have exceptionally long antennae, coarsely faceted, often closely placed eyes (separated by less than two diameters) and the reddish areas of the pronotum and elytra entirely transparent (see Vandenberg and Gordon 1988 for a more detailed comparison). The Holarctic genus *Coccinella* (Figs. 17, 18) also is allied closely to *Cycloneda. Coccinella* can be distinguished by the very different repertoire of pronotal color patterns which feature a large, subtrapezoidal or triangular white mark in each anterior pronotal angle, sometimes narrowly joined along the anterior border. *Coccinella* species also have a more robust body and appendages, and the postmetacoxal line with a sharply incised oblique line. While *Cycloneda* is restricted to the New World and has its highest concentration in the Neotropics, *Coccinella* occurs in both the Eastern and Western Hemispheres, but does not extend south of Mexico.

Species composition.—As defined here, *Cycloneda* includes species formerly assigned to *Coccinellina* and *Pseudadonia.* Timberlake (1943) provisionally transferred the following species names from *Coccinella* when he proposed the genus *Coccinellina*: *C. ancoralis* Germar, *C. areata* Mulsant, *C. emarginata* Mulsant, *C. eryngii* Mulsant, *C. fulvipennis* Mulsant, *C. lucasii* Mulsant, *C. petitii* Mulsant, *C. pulchella* Klug. He also added two new species: *Coccinellina ecuadorica* Timberlake and *Coccinellina shannoni* Timberlake. Most of the older names have accumulated a number of synonyms as reported in the most recent checklists and catalogs (Korchefsky 1932, Blackwelder 1945), but Timberlake did not investigate the priority of existing names, nor examine the type material to determine which synonyms are justified. Gordon (1987) transferred additional species names to *Coccinellina* (*C. germainii* Crotch, *C. arcula* Erichson, *C. ocelligera* Crotch), but cited Timberlake's work as the source of the change. Although Timberlake did not stipulate these additional names, he had made a general comment under his description of



Figs. 1–9. 1–3, *Cycloneda munda*. 1, Median cross-section, left elytron. 2, Head, pronotum and elytra, frontal view, male. 3, Left hind leg, ventral view. 4–6, *C. polita*. 4, Median cross-section, left elytron. 5, Head, pronotum and elytra, frontal view, male. 6, Left hind leg, ventral view. 7–9, *C. sanguinea*. 7, Median cross-section, left elytron. 8, Head, pronotum and elytra, frontal view, male. 9, Head, and pronotum, frontal view, female.

Coccinellina that "The neotropical species (except *C. transversoguttata* Fald.) which have been referred to *Coccinella* are rather different from the familiar holarctic species, . . ." (Timberlake 1943). Therefore, Gordon transferred all the remaining Neotropical species represented in the Crotch collection which had not already been removed through some other more recent revision. This was appropriate in all but the last case: *C. ocelligera* does not belong here, but should be placed in or near *Neda*.

Pseudadonia Timberlake was always a monotypic genus. Following the synonymy proposed by Chapin (1969) it contributes only *Pseudadonia fulvipennis* (Mulsant) (= *Pseudadonia chiliana* Timberlake), a species which Timberlake also had placed in *Coccinellina*. This species fits well within the generic concept of *Cycloneda* as diagnosed above, furthermore the name Pseudadonia is preoccupied by *Pseudadonia* Handlirsch 1906, a fossil mycetophilid.

The list of species retained from those formerly classified in *Cycloneda* (Blackwelder 1945) is quite small. The three North American species, *C. sanguinea, C. munda,* and *C. polita,* all belong here. The more recently described subspecies *Cycloneda sanguinea caymana* Chapin (1957) also belongs in this genus, but is distinct from *C. sanguinea.* Moreover, it overlaps in distribution with *C. sanguinea limbifer* (Chapin 1957) without forming intergrades. *Cycloneda caymana* (Chapin) (**new status**) resembles our west coast species, *Cycloneda polita* (Fig. 2), because of the similar dorsal color pattern, small size, and oval, somewhat depressed body form, but a closer relationship to *C. sanguinea* is suggested by the shared attributes of an apically knobbed basal lobe (similar to Fig. 24), and steeply descending, concave elytral epipleuron (similar to Fig. 7).

Adalia galapagoensis Van Dyke (1953) is a species from Charles Island of the Galapagoes Archipelago which also belongs to *Cycloneda* (*Cycloneda galapagoensis* Van Dyke (**new combination**)). Its original placement in *Adalia* probably is due to a misinterpretation of the configuration of the postmetacoxal line, which can be used to distinguish the two genera (see discussion under the diagnosis for *Cycloneda* and the ensuing remarks above). *Cycloneda galapagoensis* is a close relative of *Cycloneda sanguinea* (widespread on the island chain). The two species share a rounded convex body form and similar structure to the basal lobe of the male genitalia.

Cycloneda fryi Crotch and *Cycloneda bioculata* Korchefsky are two other species which belong in or near *Cycloneda. Coccinella* no. 18 in the Biologia Centrali-Americana (Gorham 1892) is an undescribed species which is better placed here than elsewhere. The elytra of this species are an unusual ashen color, and the oblique postcoxal line is more developed than in most members of *Cycloneda.*

KEY TO NORTH AMERICAN *CYCLONEDA* SPECIES

1\. Form nearly circular (Fig. 10); suprahemispherical (Fig. 8); elytral epipleuron strongly concave, steeply descending externally (Fig. 7). Female with white pronotal border strongly narrowed or interrupted anteromedially (Fig. 9); male with border entire, with median tapered prolongation extending posteriorly (Fig. 8), this mark lacking in female. Southern U.S., from North Carolina to Florida, west to Southern California, widespread in the Neotropics 2

– Form oval, slightly elongate; subhemispherical (Figs. 2, 5); elytral epipleuron weakly concave, subhorizontal (Figs. 1, 4). Both genders with white pronotal border continuous across anterior margin, with median tapered prolongation extending posteriorly (Figs. 2, 5). Widespread in North America but absent from Florida and lower part of southern most states, extending northward into southern Canada 3

2\. Lateral border of elytron clear amber (Fig. 10) . . . . *sanguinea sanguinea* (L.)

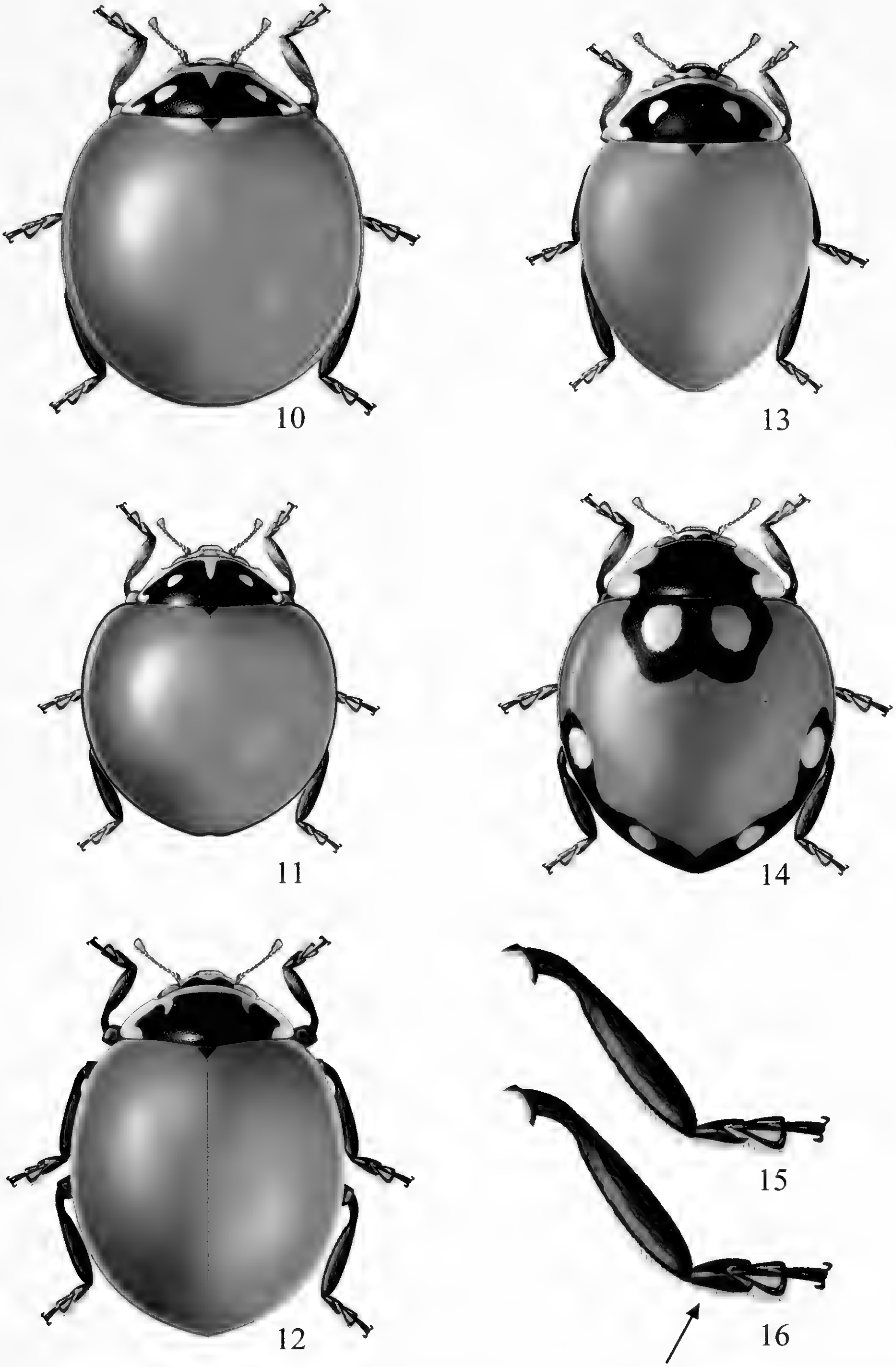
– Lateral border of elytron narrowly darkened (Fig. 11). A West Indian subspecies, also recorded from southern Florida . . . . *sanguinea limbifer* Casey

3\. Hind leg with femoral apex, tibia, and tarsus cream colored to reddish brown, rest of femur black (Fig. 3). Elytron pale orange; paler area on base of elytron, when evident, begins at scutellum and continues as narrow band around humeral angle (Fig. 2). Widely distributed in the U.S. and southern Canada east of the Rocky Mountains . . . . *munda* (Say)

– Hind leg with femoral apex, small area at base and apex of tibia, and tarsus cream colored to reddish brown, rest of femur and tibia black (Fig. 6). Elytron pale orange to dark red; paler area on base of elytron, when evident, restricted to semicircular spot adjacent to scutellum, not attaining humeral angle (Fig. 5). Widely distributed in the western U.S. and southern Canada from the Pacific coast through the Rocky Mountains . . . . *polita* Casey

Cycloneda sanguinea sanguinea (L.)
(Figs. 10, 23–25)

Coccinella sanguinea Linnaeus 1763: 10.
Daulis sanguinea: Mulsant 1850: 326.
Cycloneda sanguinea: Crotch 1871: 6; Crotch 1873a: 372; Crotch 1874: 164; Blatchley 1910: 515; Korschefsky 1932:



Figs. 10–16. 10–14, Habiti of *Cycloneda* species (male). 10, *C. sanguinea sanguinea.* 11, *C. sanguinea limbifer.* 12, *C. fulvipennis* (= *Pseudadonia chiliana,* type species of *Pseudadonia*). 13, *C. emarginata* (type species of *Coccinellina*). 14, *C. pulchella.* 15–16, Middle legs of *Cycloneda* species. 15, Middle leg of *C. emarginata* (male) showing unmodified basitarsus typical of most *Cycloneda* species. 16, Middle leg of *C. fulvipennis* (male) showing swollen basitarsus (arrow).

286; Timberlake 1943: 23; Wingo 1952: 46; Mader 1958: 241 (in key); J. Chapin 1974: 62; Phuoc and Stehr 1974: 58 (pupal description, key); Saini 1983: 392 (descriptions of larval color patterns); 1985: 5 (colored photo 4th instar larva).

Cycloneda sanguinea sanguinea: Gordon 1985: 820 (in key, diagnosis, distribution, genitalia); Gordon and Vandenberg 1993: 307 (description of 4th instar larva, larval key).

Neda sanguinea: Bruch 1915: 388.

Coccinella immaculata Fabricius 1792: 267.

Daulis immaculata: Mulsant 1850: 327.

Cycloneda immaculata: Casey 1899: 92 (in key); Gordon 1985: 820 (as synonym of *sanguinea*).

Cycloneda munda ab. *immaculata*: Mader 1958: 241.

Daulis steini Mulsant 1866: 222; Crotch 1874: 164 (as synonym of *sanguinea*) Korchefsky 1932: 286 (as synonym of *C. sanguinea* Mulsant); Gorham 1892: 170 (as synonym of *C. sanguinea* Mulsant); Blackwelder 1945: 452 (as synonym of *C. sanguinea* Mulsant).

Cycloneda polonica Hampe 1850: 357; Crotch 1874: 45 (as synonym of *C. sanguinea* Mulsant); Korchefsky 1932: 286 (as synonym of *C. sanguinea* Mulsant); Blackwelder 1945: 452 (as synonym of *C. sanguinea* Mulsant).

Cycloneda rubripennis Casey 1899: 92; Korschefsky 1932: 285 (as synonym of *munda*); Mader 1958: 241 (in key); Gordon 1985: 820 (as synonym of *sanguinea*).

Cycloneda hondurasica Casey 1899: 92; Mader 1958: 240 (in key) (examined). **New synonym.**

Coccinella reflexa Germain 1854: 333; Brèthes 1923: 454 (as synonym of *C. fulvipennis* Mulsant); Korchefsky 1932: 510 (as synonym of *C. fulvipennis* Mulsant); Blackwelder 1945: 454 (as synonym of *C. fulvipennis* Mulsant) (examined). **New synonym.**

Neda reflexa: Rivera 1904: 16 (generic reassignment, descriptions of egg, larva, pupa, habitats, prey).

Coccinellina reflexa: Chapin 1969: 467 (removed from synonymy, generic reassignment).

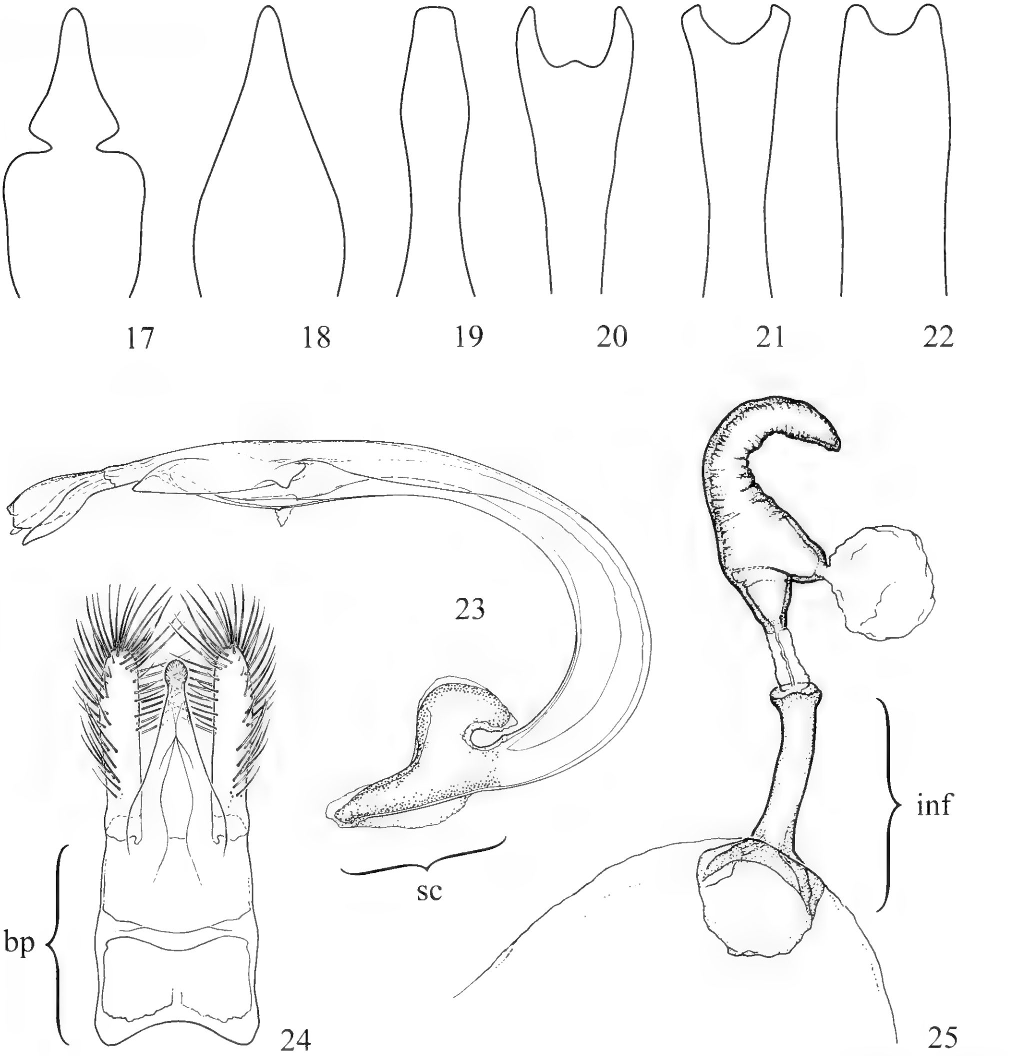
Coccinella (*Cycloneda*) *sanguinea*: Leng 1903: 202.

Coccinella (*Cycloneda*) *sanguinea* var. *immaculata*: Leng 1903: 203.

Coccinella (*Cycloneda*) *sanguinea* var. *rubripennis*: Leng 1903: 203.

Remarks.—Gordon (1985) published a synonymical bibliography for *Cycloneda sanguinea,* but did not investigate foreign material for possible unreported synonyms. Examination of the female holotype of *Cycloneda hondurasica* Casey ("Cycloneda hondurasica: Hond/CASEY bequest 1925/ TYPE USNM 35524 [red label]/Cycloneda hondurasica Csy[handwritten]/Casey determ sanguin-10") reveals that it also belongs to *C. sanguinea sanguinea.* Casey had distinguished *C. hondurasica* in his key by the presence of a short but distinct oblique line separated from the main arc of the postmetacoxal line. In the case of the type specimen, and in other specimens of *C. sanguinea* which exhibit this condition (less than 10%), it appears to be primarily a postmortem artifact resulting from a slight buckling of the abdomen upon drying. Live specimens of *C. sanguinea* often have a faint integumental wrinkle in this same position which corresponds to the area where the hind tarsus comes to rest when the appendages are withdrawn during a death feint. Rarely does this oblique feature have a sharply incised appearance as it does in the related genus *Coccinella.* No significant differences could be found from examining the type of *C. hondurasica* which would justify maintaining a separate species for this minor and possibly artificial variant. Casey, himself, designated the specimen as "sanguin-10" and placed it together with other C. *sanguinea* in a single unit tray.

Germain (1854) reported the common occurrence of adult and larval *Coccinella*



Figs. 17–25. 17–22, Basal lobes of male genitalia, characteristic of different coccinelline genera (diagrammatic). 17, *Coccinella transversoguttata* Mulsant. 18, *Coccinella monticola* Mulsant. 19, *Mulsantina* sp. 20, *Olla* sp. 21, *Neda* sp. 22, *Paraneda* sp. 23–24, Male genitalia of *Cycloneda sanguinea sanguinea*. 23, Sipho (sc = siphonal capsule). 24, Phallobase (bp = basal piece). 25, Female genitalia of *Cycloneda sanguinea sanguinea* (inf = infundibulum).

reflexa on fennel (*Foeniculum vulgare* Miller) in Santiago, Chile during the month of February. The consistency of this hostplant association led Germain to speculate that the species is phytophagous; however, his description clearly indicates a glabrous habitus, and therefore not a member of the only phytophagous subfamily in the Neotropics: Epilachninae. Brèthes (1923) placed *C. reflexa* as a synonym of *Coccinella fulvipennis* Mulsant, but provided no explanation for his action. Chapin (1969) resurrected the species and transferred it to his new genus *Coccinellina,* indicating important differences in the size and dorsal color patterns for the two nominate species. Although Chapin never examined the type material, he based his concept of *C. reflexa* on specimens taken in Arica, Chile in 1966 by Alfonso Aguilera P., which compared in detail with the type description except for a minor discrepancy in size (5 mm in length as opposed to 6.3 mm). These specimens are not to be found in the pinned collection at the USNM; however, a slide mount of the female genitalia of one of the specimens was located in Chapin's slide cabinet. These genitalia agree in all particulars with those of *Cycloneda sanguinea,* a species which ranges in length from 3.2 to 6.5 mm.

The description of the larval and pupal stages of *Coccinella reflexa* made by Rivera (1904) in Chile (as *Neda reflexa* (Germain)) is also in agreement with both published descriptions (Saini 1985, Phuoc and Stehr 1974, Gordon and Vandenberg 1993) and museum specimens of *Cycloneda sanguinea. Cycloneda sanguinea* is common in collections from Chile, and I do not know of any other very similar species from that country. In southern California, where *Cycloneda sanguinea* is common, I often have observed adults and larvae together on volunteer growths of *Foeniculum vulgare,* the very habitat specified for *C. reflexa* in Germain's original description.

The facts outlined above were compelling enough for me to propose the synonymy of *C. reflexa* even in the absence of type material. I eventually had the opportunity to examine a syntype of *Coccinella reflexa* ("CHILE [handwritten]/Coccinella reflexa Germ.[handwritten]/SINTIPO/CHILE M.N.H.N. Tipo No 2158") from the Museo Nacional de Historia Natural, Santiago, and confirm my suspicions. It is a representative female of *Cycloneda sanguinea,* with head and pronotal markings much as in the example illustrated (Fig. 9). The specimen is card mounted, and the elytra are slightly parted at the sutural apex, giving an initial impression of less convexity, which is dispelled upon closer examination. The specimen is at the upper range of body size for the species (6.3 mm), but a number of examples from Chile and Argentina boast similar dimensions.

Cycloneda sanguinea limbifer Casey
(Fig. 11)

Cycloneda limbifer Casey 1899: 92; Zelený 1969: 333 (biology, toxicology); Hodek 1973: pl. XXVII, fig. 3 (4th instar larva color illustration).

Coccinella (Cycloneda) limbifer: Leng 1903: 204.

Cycloneda sanguinea ab. *limbifera*: Korschefsky 1932: 286 (unjustified emendation of *limbifer,* ICZN 1999, Art. 31.2.1–3.2.2); Mader 1958: 241 (in key).

Cycloneda sanguinea limbifer: Chapin 1949: 23; 1957: 89; Gordon 1985: 823 (in key, distribution, diagnosis, genitalia, adult habitus); Gordon and Vandenberg 1993: 308 (description of 4th instar larva, larval key).

Remarks.—The name *Cycloneda limbifer* was applied by Casey (1899) to specimens taken from the Bahamas (Egg Island), that differ from most mainland examples of *C. sanguinea* by the presence of a narrow black border on the outer elytral margins. Authors have assigned variable rank to this insular form, from aberration to full species, a problem whose satisfactory solution may require more sophisticated genetic studies and laboratory crosses. Chapin (1957) reports *C. s. limbifer* as widely distributed in the West Indian islands as far south as St. Lucia of the Lesser Antilles. However, not all of the island forms are strictly comparable. In specimens from Cuba, Haiti, Dominican Republic, and Puerto Rico, the elytral border is always darkened, and the beetles are further distinguished from their mainland relations by possessing a shorter body form, a broader elytral base (relative to pronotal width) and a tendency towards dwarfism, particularly in males (Fig. 11). If specimens from only these islands were compared to the mainland (Fig. 10), one might conclude that *limbifer* is deserving of full species status. On the other hand, specimens from the Bahamas are much like those from the mainland except for the darkened border, and specimens from Jamaica appear somewhat intermediate in body form and the elytral border varies from black to clear amber. Various intergrades also occur along the island chains that form the Lesser Antilles, suggesting that a step cline or complex of closely related species may provide a more accurate model of the Caribbean populations.

Chapin (1949) reported two specimens of *C. s. limbifer* from Key West, Florida, but it is not clear whether the subspecies is permanently established there. Although the darkened elytral border occurs independently within the nominate subspecies, it does so only rarely in North and Central American populations. In Southern Brazil, Chile, and Argentina the extreme outer border is often either a dark reddish amber or blackish.

Cycloneda munda (Say)
(Figs. 1–3)

Coccinella munda Say 1835: 202; Crotch 1874: 107.

Daulis munda: Mulsant 1850: 324.

Cycloneda munda: Crotch 1871: 6; 1873a: 372 (as synonym of *C. sanguinea* Linnaeus); Casey 1899: 93; Leng 1920: 216; Korschefsky 1932: 284; Timberlake 1943: 23; Wingo 1952: 46; Mader 1958: 241 (in key); J. Chapin 1974: 63; Phuoc and Stehr 1974: 58 (pupal description, key); Gordon 1985: 820 (in key, distribution, diagnosis, genitalia, adult habitus); Gordon and Vandenberg 1993: 308 (description of 4th instar larva, larval key).

Coccinella (*Cycloneda*) *sanguinea* var. *munda*: Leng 1903: 203.

Cycloneda ater Casey 1899: 93; Gordon 1985: 820 (examined). **New synonym.**

Cycloneda atra Casey 1908: 405; Leng 1920: 216.

Coccinella krikkeni Iablokoff-Khnzorian 1982: 395 (examined). **New synonym.**

Remarks.—Crotch's confusion over the taxonomic boundaries of *Cycloneda* and its included species is nowhere more apparent than in his variable treatment of *C. munda* which he initially transferred from *Coccinella* to his newly established genus *Cycloneda* (Crotch 1871), placed as a synonym of *Cycloneda sanguinea* in his revision of the Coccinellidae of the United States (Crotch 1873a), omitted in a subsequent checklist of the Coleoptera of America, north of Mexico (Crotch 1873b), and then resurrected as a valid species and returned to the genus *Coccinella* in his World revision (Crotch 1874). Crotch's vacillating perspective was probably due to the conflicting impressions provided by *C. munda*'s external color pattern (very like that of *C. sanguinea*) and the external topology (more elongated and depressed than most of its congeners). The similarity in the form of the genitalia of *C. sanguinea* and *C. munda* (Gordon 1985) resolve this apparent dilemma and support the view of a very close systematic relationship.

Casey (1899) described *Cycloneda ater* (later corrected to *atra*) from an unlabeled specimen found in the Levette cabinet. While Casey later expressed some doubt regarding the proper generic placement of the unusual all black species (Casey 1908), he felt certain it was a member of the North American fauna because the cabinet contained "little or no foreign material." Other revisions, confined to the Nearctic fauna (Leng 1903, 1920; Gordon 1985), skirted the issue of classification by declaring the specimen to be of probable foreign origin; a not unreasonable assumption considering the species failed to reappear in any other collected samples. Recent dissection and examination of the male holotype ("atra Csy[handwritten]/bequest 1925/TYPE USNM 35528 [red label]") reveal it to be a wholly typical example of *Cycloneda munda* in all respects except for the aberrant coloration. Not only are the chitinous external structures and genitalia deeply pigmented, but the internal ligaments and fat body are sooty and oddly decomposed. Thus, it would seem that the black coloration is more likely due to some sort of postmortem treatment than an expression of genetics. Backlighting the elytra with a strong light reveals a ruddy glow, suggesting the presence of the orange pigmentation found in typical examples of the species.

Iablokoff-Khnzorian described *Coccinella krikkeni* from a male specimen deposited in Naturalis, Nationaal Natuurhistorisch Museum, Leiden, and published the description, along with illustrations of the habitus and male genitalia, in a large volume on Palearctic and Oriental Coccinellinae (Iablokoff-Khnzorian 1982). While the genitalia of some *Coccinella* species are not very different from those of *Cycloneda,* the pronotal color patterns of *C. krikkeni* are highly aberrant for *Coccinella,* yet typical of *Cycloneda.* The genitalia illustrations and description of leg coloration suggest the species *Cycloneda munda,* which is restricted to the eastern United States and parts of Canada. Subsequent examination of the holotype ("Museum Leiden, S. INDIA madras State, Coimbatore, 1400 ft, X.1961 P.Susai Nathan/Holotypus Coccinella Krikkeni Khnz [handwritten label]") confirmed the suspected synonymy, but provided no insight as to how it came to bear such an unexpected locality label. This unique record may be the result of accidental transport through commerce, or, more likely, an accident of mislabeling.

Cycloneda polita Casey
(Figs. 4–6)

Cycloneda polita Casey 1899: 93; Timberlake 1943: 24; Mader 1958: 241 (in key); Hatch 1961: 181; Belicek 1976: 330; Gordon 1985: 820 (in key, distribution, diagnosis, genitalia, adult habitus); Gordon and Vandenberg 1993: 309 (description of 4th instar larva, larval key).

Coccinella (*Cycloneda*) *sanguinea* var. *polita*: Leng 1903: 203.

Coccinella (*Cycloneda*) *sanguinea*: Palmer 1914: 232 (not *sanguinea* Linnaeus) (description larval instars, color habitus late instar).

Cycloneda munda ab. *polita*: Leng 1920: 216; Korschefsky 1932: 285.

Cycloneda polita flava Timberlake 1943: 24.

Remarks.—Gordon synonymized the subspecies *Cycloneda polita flava* Timberlake with the nominate subspecies because it has identical genitalia, and differs only in possessing a paler elytral coloration. Although I disagree with the reasons for the synonymy, the action is still supportable. Specimens of *Cycloneda polita* with bright orange or scarlet elytra also occur within the specified range of *C. polita flava* (Alameda Co. and Santa Cruz Mountains, California); therefore, it is probably little more than an aberration which occurs at higher frequencies in some areas.

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NOTE

New Data on the Structure of the Female Genitalia of Flea Beetles (Coleoptera: Chrysomelidae)

Female genitalia of flea beetles have received much attention during last two decades and have become an important source of valuable diagnostic and phylogenetic characters (Cox 1997; Doguet 1994; Duckett 1999; Kangas and Rutanen 1993; Konstantinov 1987, 1998a, 1998c; Konstantinov and Vandenberg 1996; Lingafelter and Konstantinov 2000). They also became a subject of comparative morphological studies (Duckett 1995; Konstantinov 1994, 1998b; Konstantinov and Rusakov 1993). As a result of these studies the structure and variability of the spermatheca, vaginal palpi and tignum are relatively well understood, however the relative position of these structures, especially in regards to the gut, tergite 9 and vagina, and the way in which they are connected to each other remained unknown.

This note intends to answer the aforementioned questions. In addition to standard dissecting techniques (Konstantinov 1998c, Lingafelter and Konstantinov 2000), "Chlorazol Black" was used to stain the membranes of the genitalia. That procedure revealed that each sclerite (tergite and sternite) consists of two membranous layers (Figs. 1A, B): an external layer (Fig. 1B thicker lines) usually more sclerotized in both tergites and sternites; and an internal layer usually much less sclerotized and fully membranous (Fig. 1B thinner lines). This latter layer usually is very poorly visible without staining. In tergites the external, dorsal layer is more sclerotized than the ventral one, whereas in sternites ventral layer is external and more sclerotized than the internal, dorsal layer. The ventral layer of sternite 8 also contains a long sclerotized projection called the tignum. The internal membranous layer connects the distal part of the more external sclerite with the proximal part of the following sclerite, thus enabling the genitalia to protrude telescopically out of the abdomen. The maximum distance to which genitalia can be protruded depends upon the length of the internal layers of segment 7, the external and internal layers of segments 8 and 9, and the distance between the base of the vaginal palpi and apex of tergite 9. The internal layer of tergite 8 forms at least the dorsal side of the gut. It also connects with the dorsal layer of tergite 9 which is situated only slightly below the dorsal side of the gut and which lateral sclerotizations are situated laterally of anus. The internal membrane of tergite 9 also extends into the ventral and lateral walls of the gut. The membranous ventral wall of the gut bends anteriorly and continues on the dorsal side of the vagina. The vaginal palpi are formed by the invagination of the dorsal side of the vagina, so their cavity opens in the body cavity. The ventral side of the vagina is a continuation of the internal layer of sternite 8. In addition the external and internal layers of tergite and sternite 8 are laterally connected to each other. The connections of the internal layers of segment 8 form lateral folds which continue on the side of the vagina.

This observation yields the rather unexpected result that the vagina is formed by membranous parts of both segments 8 and 9. In order to avoid this interpretation, we would have to assume that tergite 9 is absent in flea beetles and everything between the external layer of tergite 8 and the vagina belongs to the internal layer of tergite 8. Although this latter explanation is the most parsimonious it should be tested by embryological or comparative morphological studies. Until then the question of the ho-

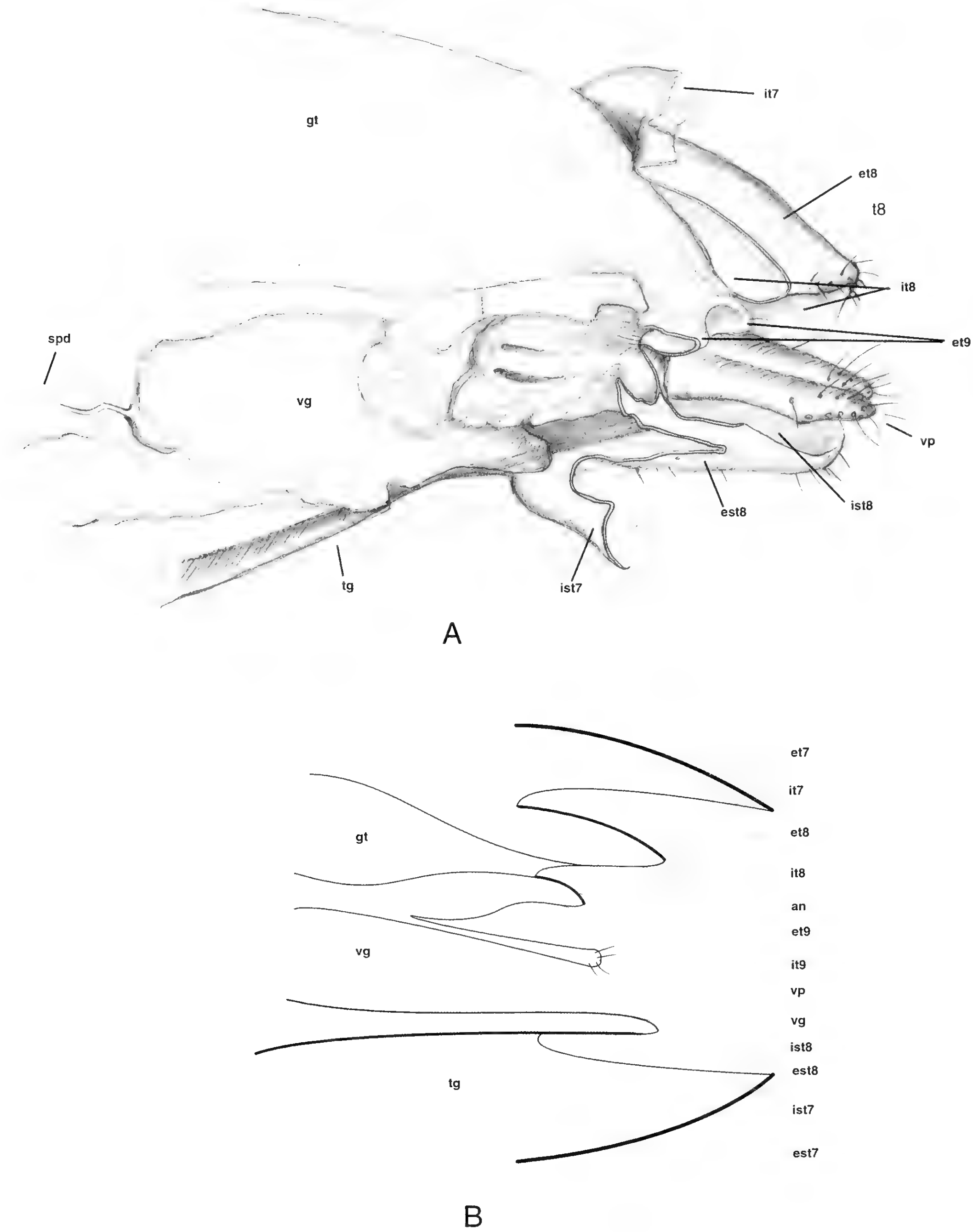

Fig. 1. Female genitalia of *Pseudodera xanthospila* Baly. A, Three dimensional drawing with right side of several sclerites removed. B, Diagrammatic sagittal section. Abbreviations: an = anus; est7 = external layer of sternite 7; est8 = external layer of sternite 8; et7 = external layer of tergite 7; et8 = external layer of tergite 8; et9 = external layer of tergite 9; ist7 = internal layer of sternite 7; ist8 = internal layer of sternite 8; it7 = internal layer of tergite 7; it8 = internal layer of tergite 8; it9 = internal layer of tergite 9; gt = gut; spd = spermathecal duct; tg = tignum; vg = vagina; vp = vaginal palpus.

mology of the vaginal palpi remains unanswered.

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NOTE

Reinstatement of *Rhithrogena manifesta* Eaton (Ephemeroptera: Heptageniidae)

The name *Rhithrogena manifesta* Eaton, 1885, was based on certain adult heptageniid mayfly specimens collected from Rock Island, Illinois in the early 1860s by B. D. Walsh. Walsh (1862) misidentified those specimens as *Baetis debilis* Walker (a species now in the genus *Paraleptophlebia* Lestage). Eaton (1885), as was his practice at the time, did not designate type specimens for his species, and any *de facto* syntypes of *R. manifesta* have been heretofore undocumented. Walsh's collections, in general, were deposited in the Chicago Museum (subsequently destroyed in the Great Chicago fire of 1871) or with H. Hagen in Prussia (subsequently placed in the Museum of Comparative Zoology, Harvard University [MCZ]) (see Burks 1953). *Rhithrogena manifesta* was placed with species in the genus *Heptagenia* Walsh by McDunnough (1924), who originally believed the genus *Rhithrogena* Eaton was equivalent with *Heptagenia.* Although McDunnough (1926) later recognized some species in *Rhithrogena,* Eaton's *manifesta* has continued to be regarded as *Heptagenia manifesta.* This is because McDunnough (1924) suggested that *H. manifesta* was related to particular species of *Heptagenia,* which more recently have been transferred to the genus *Nixe* Flowers. Flowers (1980) chose not to place *H. manifesta* in *Nixe* until more was known about the species. The only other report of the occurrence of the species was from Quebec by Walley (1927). McCafferty (1996) treated *H. manifesta* as a *nomen dubium* because of the many uncertainties surrounding it.

Recently, we located and studied four adult specimens in the MCZ that Walsh had collected from Rock Island in 1860 and 1863 and identified as *B. debilis.* These specimens were consistent with Eaton's description of *manifesta.* We also discovered and studied a series of 15 adult specimens from New Brunswick and Quebec in the Canadian National Collection of Insects, Agriculture and Agri-Food Canada (CNC) that had been identified as *H. manifesta* by McDunnough. We found the CNC specimens to be the same species as those in the MCZ and thus correctly identified by McDunnough. Our study of these two series of specimens also revealed important additional data regarding the species. It was clear that the species belongs in the genus *Rhithrogena,* as Eaton (1885) had originally surmised, not in *Heptagenia.* Also, whereas the species fits the rather incomplete description given by Eaton (1885), the species also fits the more completely defined and relatively well-known species *R. pellucida* Daggy (Daggy 1945, Burks 1953, Leonard and Leonard 1962, McShaffrey and McCafferty 1988, Durfee and Kondratieff 1994). *Rhithrogena pellucida* is a relatively widespread North American species that also is known from the vicinity of the type locality of Eaton's species (Randolph and McCafferty 1998, Durfee and Kondratieff 1994). Our study of comparative material showed it to be the same as *H. manifesta.*

Based on the above observations, four steps are now required to remediate the taxonomic and nomenclatural problems associated with *H. manifesta.* First, we replace the species to its proper genus, as *Rhithrogena manifesta* Eaton (recombination). Second, we place *R. pellucida* as a subjective junior synonym of *R. manifesta* (**new synonym**). Third, we designate a lectotype from the Rock Island material collected by Walsh (see material examined below) for the purpose of fixing the identity of *R. manifesta.* Fourth, we remove *R. manifesta* from *nomen dubium* status. It should be noted that although Eaton (1885) listed *R. manifesta* as a renaming, *R. manifesta* was technically a new name. Walsh (1862) did not describe *B. debilis* as new. Thus, no secondary homonym of that name should be construed, as might be incorrectly interpreted from the synonymy given by Eaton (1885) for *R. manifesta.*

Material examined.—*Rhithrogena manifesta:* lectotype, 1 ♂ adult, Illinois, Rock Island, 1863, Walsh [MCZ]. Other material: 1 ♂ adult, Illinois, Rock Island, Walsh [MCZ]; 1 ♀ adult, Illinois, Rock Island, 1860, Walsh [MCZ]; 1 ♀ adult, Illnois, Rock Island, Walsh [MCZ]; 1 ♂ adult, 6 ♀ adults, New Brunswick, Fredericton, VII-1928, W. J. Brown [CNC]; 1 ♀ adult, Quebec, Cascades Point, 30-VIII-1930, L. J. Milne [CNC]; 2 ♂ adults, same data but 26-VII-1930 (one set genitalia on slide) [CNC]; 1 ♀ adult, Quebec, Kirk's Ferry, 4-VII-1925, G. S. Walley [CNC]; 1 ♀ adult, Quebec, Lachine, 6-VIII-1924, G. S. Walley [CNC]; 2 ♂ adults, Quebec, Laprarie, 21-VII-1925, F. P. Ide [CNC]; 1 ♀ adult, Quebec, Richelieu, 5-VII-1927, G. S. Walley [CNC].

Rhithrogena pellucida: 1 ♂ adult, 1 ♀ adult, Indiana, West Lafayette, 13-VII-1974, H. R. Lawson [Purdue Entomological Research Collection, West Lafayette, Indiana].

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NOTE

Variation in Abdominal *sa*2 and *sa*3 Setation in Larvae of *Arctopsyche grandis* (Banks) (Trichoptera: Hydropsychidae)

Arctopsyche grandis (Banks) is the most abundant and widespread of the western Nearctic arctopsychine caddisflies, and the larvae are often collected in streams from 45–2,150 m in elevation (Givens and Smith 1980). Wiggins (1996) separated known larvae of *Arctopsyche* from larvae of the genus *Parapsyche* by the setation of the abdominal *sa*2 and *sa*3 positions. *Parapsyche* species bear a tuft of several long setae or scale hairs in each position, whereas *Arctopsyche* species bear a single, long, hair-like seta in each position, occasionally accompanied by one or two shorter setae.

To quantify the extent of variation in the abdominal setation in *A. grandis,* I examined larvae from four Rocky Mountain rivers: the Clark Fork River in Montana, the Arkansas and Eagle rivers in Colorado, and the Red River in New Mexico. Benthic macroinvertebrate samples for ecological studies had been taken from 1994 to 1996 at 8–14 individual sites in each river. A total of 660 *A. grandis* larvae were examined, and the number of setae in each of the *sa*2 and *sa*3 positions of abdominal segments I–VII was counted. The geometric mean number of setae per position was calculated, and these data were analyzed by general linear methods analysis of variance (GLM-ANOVA) using NCSS (Number Cruncher Statistical Systems 1997) to determine if statistical differences existed in setation between abdominal segments, setal positions, or river systems. A 95% significance level (α = 0.05) was used for all tests.

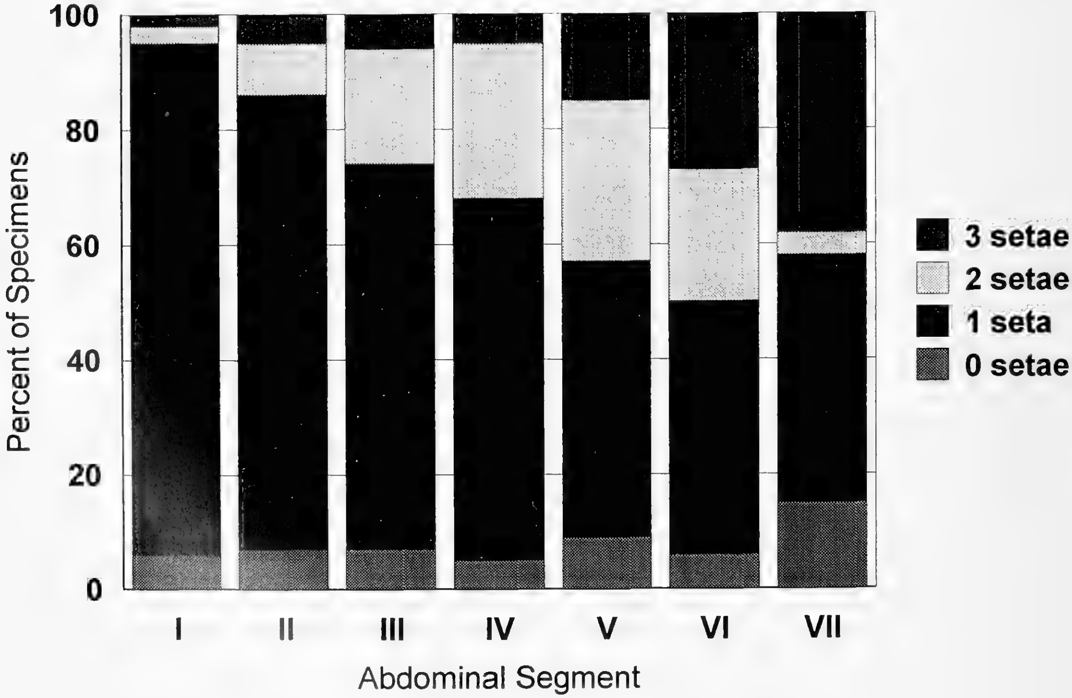

Fig. 1. Number of setae in *sa*2 position on abdominal segments of *Arctopsyche grandis* (n = 660).

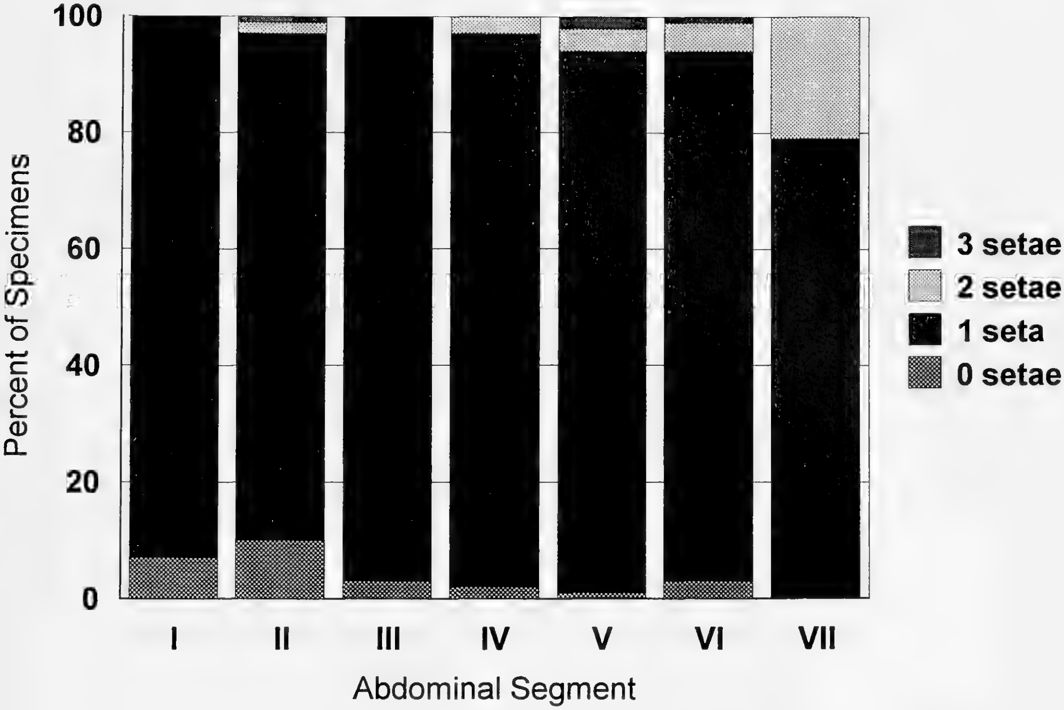

Fig. 2. Number of setae in *sa*3 position on abdominal segments of *Arctopsyche grandis* (n = 660).

Number of setae ranged from 0–3, and most positions were occupied by only one seta (Figs. 1, 2). The *sa*2 positions were significantly more likely to have 0, 2, or 3 setae than the *sa*3 positions ($P < 0.001$; F = 21.79; df = 4,51), and ANOVA demonstrated significant differences ($P < 0.05$) between positions in each of abdominal segments II–VI. Posterior abdominal segments (IV–VII) were significantly more variable in numbers of setae than anterior abdominal segments (I–III) in both *sa*2 ($P = 0.013$; F = 3.61, df = 4,23) and *sa*3 ($P < 0.001$; F = 8.11; df = 4,23) positions. When 2 or 3 setae were found in a single position, one was usually of normal length and the extra setae were always reduced in size. All setae in all positions were hairlike. There were no significant differences observed between setation of larvae from the four individual river systems ($P = 0.851$; F = 0.26; df = 4,23).

This report confirms Wiggins' (1996) observations on the number and form of setae in the abdominal *sa*2 and *sa*3 positions in *A. grandis* larvae, but further identifies and quantifies between-segment and between-position variation not previously noted.

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NOTE

Eucoloneura, A New Name to Replace the Generic Homonym *Coloneura* Davis (Lepidoptera: Psychidae)

Because *Coloneura* Davis (1964. United States National Museum Bulletin 211: 89; type species, *Coloneura fragilis* (Barnes and McDunnough) is preoccupied by *Coloneura* Foerster (1862. Decheniana (Naturhistorischer Verein der Rheinlande)—Biologische Abeilung 19: 276), I am proposing the **new name *Eucoloneura*** to replace the junior homonyn *Coloneura* Davis. *Coloneura* Foerster was proposed for a genus of Braconidae (Hymenoptera). *Eucoloneura* is to be considered feminine in gender.

Donald R. Davis, *Department of Systematic Biology, Smithsonian Institution, Washington, DC 20560-0127, U.S.A. (e-mail: davis.don@nmnh.si.edu)*

PROC. ENTOMOL. SOC. WASH.
104(1), 2002, pp. 245–246

OBITUARY

Robert Judson Lyon
1918–2000

It is with great regret that I announce the death of hymenopterist Robert J. Lyon (June 29, 1918 to December 24, 2000). Despite a full-time teaching schedule at Los Angeles City College, he made major contributions to our knowledge of taxonomy and biology of Cynipidae.

Bob attended the University of Texas at El Paso on a music scholarship and played in the university's marching band. He received a bachelors degree in zoology in 1941, soon afterward joining the Army Air Corps to serve in World War II. After the war he continued his education, receiving a master of science degree from the University of Southern California. He began a doctoral program in entomology at the University of California at Los Angeles and, during these studies, had the opportunity to visit and do research at the National Museum of Natural History, Smithsonian Institution, and where he met Lewis Weld, also a cynipid specialist.

Bob married his first wife, Kathrine, in 1948, with whom he had two sons, Mark and Gary, and a daughter, Stephanie. Bob gave up his doctoral work at UCLA so he could spend more time with his family, and he began a teaching career at Los Angeles City College where he soon advanced to department chairman. While fully involved in teaching, Bob continued corresponding with Weld and researching cynipidae. This research was assisted when Weld bequeathed his extensive personal collection of Cynipoidea specimens and literature to Bob.

Bob overcame some major personal tragedies, such as the breakup of this marriage and the death of his teenaged son Gary. In 1970 Bob married again, this time to Devie Ruben, who bore him two sons, Barry and Richard. That happiness lasted 21 years before Devie succumbed to liver cancer while their youngest son, Richard, was still in high school. During his last years, Bob had the joy of seeing two granddaughters, Sherry Garsow and Cassandra Lyon.

Bob was a wonderful colleague, faithful correspondent and careful taxonomist. He encouraged and assisted many others working on Cynipoidea and was generous in loans of material from the Weld collection as well as his own personal collection. During his final months, he arranged for his and Weld's collections to be given to the California Academy of Sciences upon his death so that this valuable material would be readily available to other scholars. He will be much missed by the entomological community.

SIGNIFICANT PUBLICATIONS

1959. An alternating, sexual generation in the gall wasp *Callirhytis pomiformis* (Ashm.) (Hymenoptera, Cynipidae). Bulletin of the Southern California Academy of Sciences 58(1): 33–37.

1963. The Alternate Generation of *Heteroecus pacificus* (Ashmead) (Hymenoptera, Cynipoidea). Proceedings of the Entomological Society of Washington 65(3): 250–254.

1964. The Alternate Generation of *Callirhytis agrifoliae* (Ashmead) (Hymenoptera: Cynipoidea). Proceedings of the Entomological Society of Washington 66(3): 193–196.

1969. The Alternate Generation of *Callirhytis quercussuttoni* (Bassett) (Hymenoptera: Cynipoidea). Proceedings of the Entomological Society of Washington 71(1): 61–65.

1970. Heterogony in *Callirhytis serricornis* (Kinsey) (Hymenoptera: Cynipoidea). Proceedings of the Entomological Society of Washington 72(2): 176–178.

1984. New cynipid wasps from California (Hymenoptera: Cynipidae). Pan-Pacific Entomologist 60(4): 289–296.

1993. Synonymy of two genera of cynipid gall wasps and description of a new genus (Hymenoptera: Cynipidae). Pan-Pacific Entomologist 69(2): 133–140.

1996. New cynipid wasps from the southwestern United States (Hymenoptera: Cynipidae). Pan-Pacific Entomologist 72(4): 181–192.

1998. (with J. N. Lund and J. R. Ott as lead authors) Heterogony in *Belonocnema treatae* Mayr (Hymenoptera: Cynipidae). Proceedings of the Entomological Society of Washington 100(4): 755–763.

SPECIES DESCRIBED BY ROBERT J. LYON

Andricus bakkeri Lyon 1984—named for Gerhard Bakker
Andricus reticulatus Lyon 1984
Antron daileyi Lyon 1996—named for Charles Dailey
Antron franklinensis Lyon 1996
Antron madera Lyon 1996
Ceroptres snellingi Lyon 1996—named for Roy Snelling
Euxystostera campanulatum Lyon 1993
Heteroecus crescentus Lyon 1984
Heteroecus devorus Lyon 1984—named for his wife, Devie
Neuroterus chrysolepis Lyon 1984
Phylloteras lyratum Lyon 1993
Phylloteras prinum Lyon 1993
Xanthoteres pungens Lyon 1996
Xanthoteres tuckeri Lyon 1996—named for John Tucker

Kathy Schick, *Essig Museum of Entomology, 201 Wellman Hall, 3112, University of California, Berkeley, CA 94720-3112, U.S.A. (e-mail: kaschick@uclink.berkeley.edu)*

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When referring to references in text, use the following; Henry (1990), (Henry 1990), (Henry 1987, 1990), (Smith 1990, Henry 1992), (Smith 1990; Henry 1990, 1991), (Miller 1990a, 1990b) where two articles are published by the same author in the same year, or Henry et al. 1990 where more than two authors are involved (do not italicize "et al."). Citations "in press" should be cited as "in press," not with year of expected publication.

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PLEASE SEE PP. 247–248 OF THE JANUARY 2002 ISSUE FOR INFORMATION REGARDING PREPARATION OF MANUSCRIPTS.

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A REVISION AND PHYLOGENETIC STUDY OF *ACTOCETOR* BECKER (DIPTERA: EPHYDRIDAE)

TORSTEN DIKOW AND WAYNE N. MATHIS

(TD) Universität Rostock, Germany; National Museum of Natural History, Research Training Program, Smithsonian Institution, Washington, D.C. 20560-0169, USA (e-mail: torsten.dikow@stud.uni-rostock.de); (WNM) Department of Systematic Biology, Entomology Section, NHB 169, Smithsonian Institution, Washington, D.C. 20560-0169, USA (e-mail: mathis.wayne@nmnh.si.edu)

Abstract.—The genus *Actocetor* Becker is revised, including a phylogenetic analysis of the seven recognized species. Two new species, ***Actocetor afrus*** (Liberia and Senegal) and ***A. yaromi*** (Ethiopia), are described. *Actocetor hendeli* de Meijere, *A. margaritatus* (Wiedemann), and *A. panelii* Frey are **new junior synonyms** of *A. indicus* (Wiedemann), and *A. beckeri* de Meijere and *A. elegans* Hendel are **new junior synonyms** of *A. nigrifinis* (Walker). Lectotypes, all females, are designated for the following species: *Notiphila indica* Wiedemann, *Ephydra margaritata* Wiedemann, *Opomyza nigrifinis* Walker, and *Actocetor beckeri* de Meijere. The cladistic analysis is based on 29 morphological characters and resulted in 10 equally most parsimonious trees (length of 60 steps and consistency and retention indices of 0.83 and 0.83 respectively). Three trees then resulted from application of successive weighting, and from these a strict concensus tree was derived that is typologically identical to one of the original 10 trees. From the consensus cladogram, the following hypotheses can be made: (1) *Actocetor* is monophyletic and (2) the subgenera *Actocetor* Becker (4 species) and *Poecilostenia* Bezzi (3 species) are each monophyletic. Although we suggest an Afrotropical origin for *Actocetor,* the genus could have resulted from speciation events in the Oriental Region. Keys for the identification of all genera of Discomyzini and the species of *Actocetor* are provided. The distribution of all species of *Actocetor* and the biology of *A. indicus* from a coastal site in Israel are discussed.

Key Words: *Actocetor,* Discomyzini, Ephydridae, phylogeny

Shore flies are attractive to study because they are ". . . a family of flies in the full flower of its evolution" (Oldroyd 1964: 189). Although appealing for research, many nonspecialists consider the adults to be rather drab, being nondescript, usually dark colored, and tiny. There are a few large shore-fly species (>5 mm), and others are comparatively pale colored, but with few exceptions, the drab generalization holds. One notable exception is the genus *Actocetor* Becker, which comprises species with spotted wings and beautifully colored bodies. Like most shore-fly species, however, specimens of *Actocetor* are generally small, with body lengths of usually less than 3.5 mm. This paper is a revision of this distinctive genus.

Although specimens of *Actocetor* are easily recognized by their unique coloration and spotted wings, the species have never been treated comprehensively, and no key

Fig. 1. Color habitus of *Actocetor indicus* (Wiedemann).

is available for all included species. Lacking adequate identification tools, some species were described more than once, sometimes from single females. The objectives of this revision are: (1) to clarify and redescribe all known species, (2) to investigate the phylogenetic relationships among them, (3) to summarize what we know about their biology, distribution, and biogeography, and finally (4) to present a key and illustrations for their identification. A key to the genera of the tribe Discomyzini Acloque is also presented.

Actocetor is known only from the Old World where the genus occurs primarily in the tropical zones of the Afrotropical and Oriental Regions. The most widely occurring species, *A. indicus* (Wiedemann; senior synonym of *A. margaritatus* (Wiedemann)), which is found in the Afrotropical, Oriental, and southern Palearctic Regions, is relatively well known because of its beautiful coloration and spotted wings. Not surprisingly, this species has been reported relatively often in the literature (see species' synonymy). The literature on the other species is meager at best, and virtually nothing about their natural history is recorded in the literature.

The nomenclatural history of *Actocetor* as a genus is mostly confined to the 20th Century when Becker (1903) first proposed the genus with *A. margaritatus* (= *A. indicus*) as its type species. The only generic synonym is *Poecilostenia* Bezzi (1908), which has been given generic or subgeneric status with the latter being more common in recent treatments and catalogs (Wirth 1955, Cogan 1980, Mathis and Zatwarnicki 1995).

The nomenclatural history at the species level, however, is more convoluted, with the type species being an example. Wiedemann (1830) named the type species in the genus *Notiphila,* apparently without realizing that six years earlier (1824) he had described the same species as *Ephydra indica.* This same species was described a third time (Hendel 1917) but using a preoccupied name, *A. beckeri.* De Meijere (1924) recognized the preoccupation and proposed *A. hendeli* as a replacement name. Frey (1958b) described this species yet again, but as a subspecies, *A. margaritatus panelii,* from specimens collected on the Cape Verde Islands. Two other species, *A. nigrifinis* (Walker) and *A. decemguttatus* (Bezzi), have similar histories, each having been described three times. Specimens of these three species are the most common in collections. The nomenclatural histories of the remaining four species of *Actocetor* are relatively uncommon, and correspondingly, not encumbered with synonyms.

METHODS AND MATERIALS

The descriptive terminology, with the exceptions noted in Mathis (1986) and Mathis and Zatwarnicki (1990a), follows that published in the *Manual of Nearctic Diptera* (McAlpine 1981). Because specimens are small, usually less than 3.5 mm in length, study and illustration of the male terminalia required use of a compound microscope. We have followed the terminology for most structures of the male terminalia that other workers in Ephydridae have used (see references in Mathis 1986, and Mathis and Zatwarnicki 1990a, 1990b), such as surstylus, which in Dryxini is divided into a presurstylus (surstylus) and postsurstylus (clasper). Zatwarnicki (1996) has suggested that the pre- and postsurstylus correspond with the pre- and postgonostylus and that the subepandrial plate is the same as the medandrium. The terminology for structures of the male terminalia is provided directly on Figs. 30–32 and 37–38 and is not repeated for comparable illustrations of other species. Species' descriptions are composite and not based solely on the holotypes. One head and two venational ratios that are used in the descriptions are defined below (all ratios are based on three specimens: the largest, smallest, and one other. Gena-to-eye ratio is the genal height measured at the maximum eye height/eye height. Costal vein ratio is the straight line distance between the apices of R_{2+3} and R_{4+5}/distance between the apices of R_1 and R_{2+3}. M vein ratio is the straight line distance along vein M between crossveins dm-cu and r-m/distance apicad of dm-cu.

The phylogenetic analysis was performed using Hennig86©, a computerized algorithm that produces cladograms by parsimony. Character data were polarized using outgroup procedures. Although autapomorphies were not included in the cladistic analysis (they were made inactive), which would skew the consistency and retention indices, we listed them on the cladogram and included them as part of generic treatments and phylogenetic considerations to document the monophyly of the lineages, particularly at the generic level.

Although most specimens are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), we also borrowed and studied numerous specimens from the following museums:

AMNH	American Museum of Natural History, New York, USA.
BMNH	The Natural History Museum (formerly the British Museum (Natural History)), London, England, United Kingdom.
CANZ	Personal collection of Silvano Canzoneri, Venezia, Italy, now in Museo Regionale di Scienze Naturali (MRSN), Torino, Italy.
CNC	Canadian National Collection, Ottawa, Canada.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MRAC	Musée Royal de l'Afrique Centrale (Koninklijk Museum voor Midden Afrika), Tervuren, Belgium.

MRSN	Museo Regionale di Scienze Naturali, Torino, Italy.
MZH	Museum Zoological Helsinki, Helsinki, Finland.
NMSA	Natal Museum, Pietermaritzburg, South Africa.
NMW	Naturhistorisches Museum, Wien, Austria.
NMWL	National Museum of Wales, Cardiff, Wales, United Kingdom.
SMN	Staatliches Museum für Naturkunde, Stuttgart, Germany.
TAU	Tel-Aviv University, Tel-Aviv, Israel.
UZMC	Zoologisk Museum, Copenhagen, Denmark.
ZIL	Zoological Institute, Lund University, Lund, Sweden.
ZMAN	Instituut voor Taxonomische Zoologie, Zoölogisch Museum, Universiteit van Amsterdam, The Netherlands.
ZMHB	Zoologisches Museum, Humboldt Universität, Berlin, Germany.

SYSTEMATICS

TRIBE DISCOMYZINI

Discomyzini Acloque 1897: 486. Type genus: *Discomyza* Meigen 1830.

KEY TO GENERA OF DISCOMYZINI

1. Vein R_{2+3} lacking a subapical stump vein . . 3
– Vein R_{2+3} bearing a subapical stump vein . . 2
2. Vein R_{4+5} basad of crossvein r-m bearing at most 1–2 tiny, black setulae; wing with irregular, transverse, wide white and brown bands; tibiae yellowish with brown rings; abdomen with maculate pattern of gray and brown microtomentum . . . . *Eremomusca* Mathis
– Vein R_{4+5} basad of crossvein r-m bearing 5–6 setae; wing generally dark with pattern of white spots; tibiae and femora unicolorous, lacking bands; abdomen mostly shiny, lacking maculate pattern . . . . . *Trypetomima* de Meijere
3. Wing hyaline or with anterior margin darkened but not spotted 5
– Wing generally dark with a pattern of white spots 4
4. Facial setae 3–5 but usually 4, all well developed; 1st flagellomere short, length subequal to height of pedicel; pseudopostocellar setae as well developed as large, proclinate, fronto-orbital seta; legs unicolorous . . . . *Actocetor* Becker
– Facial setae 2, only dorsal seta well developed; 1st flagellomere longer than height of pedicel; pseudopostocellar setulae distinctly smaller than large proclinate fronto-orbital seta; tibia or tarsus generally paler colored than femur . . . . *Guttipsilopa* Wirth, subgenus *Guttipsilopa*
5. Alula weakly developed, very narrow 9
– Alula well developed, earlike 6
6. Intrafrontal seta present; fronto-orbital setae 4 (anterior 2 setae proclinate, 3rd lateroclinate, 4th laterorectinate) . . . . . . *Paratissa* Coquillett
– Intrafrontal seta absent; fronto-orbital setae 2–3 7
7. Supra-alar seta well developed, length subequal to postalar seta . . . . *Rhysophora* Cresson
– Supra-alar seta moderately well developed, length about half postalar seta 8
8. Arista bearing 3–5 dorsal rays; facial setae 2, both inserted on ventral 3rd of face; vein R_{4+5} basad of crossvein r-m bearing 3–4 black setulae; legs unicolorous . . . . *Hostis* Cresson
– Arista bearing 7–9 dorsal rays; facial setae sometimes 2 but usually 4 (becoming larger dorsally; sometimes with larger gap between dorsalmost seta and those ventrad) in a vertical row that extends dorsad to midfacial height; vein R_{4+5} basad of crossvein r-m bare; legs dark with yellow tarsus, apical tarsomere dark . . . . *Guttipsilopa* Wirth, subgenus *Nesopsilopa* Mathis and Wirth
9. Prescutellar acrostichal seta absent; katepisternal seta 1; facial setae 3–5, all small and poorly developed; face conspicuously and deeply, transversely rugose; only the reclinate fronto-orbital seta well developed . . . . *Discomyza* Meigen
– Prescutellar acrostichal seta present; katepisternal setae 2, dorsal seta larger; facial setae 2, dorsal pair cruciate, ventral pair poorly developed; face at most with shallowly impressed, transverse striae; at least 1 proclinate fronto-orbital seta in addition to reclinate seta well developed 10
10. Pseudopostocellar setae well developed, length about ½ that of ocellar setae, divergent at usually less than 90° . . . . *Clasiopella* Hendel
– Pseudopostocellar setae weakly developed, length considerably less than ½ that of ocellar setae, orientation variable 11
11. Eye appearing bare; 1 well-developed proclinate fronto-orbital seta (2nd seta greatly reduced) inserted anterior of reclinate seta; presutural supra-alar seta weakly developed,

length less than anterior notopleural seta (except in *M. cressoni* Lizarralde de Grosso); vein R_{4+5} basad of crossvein r-m bearing 2 setulae; legs bicolored . . . *Mimapsilopa* Cresson

– Eye conspicuously setulose; 2 well-developed proclinate fronto-orbital setae, anterior proclinate seta at about same level as large, reclinate seta, posterior proclinate seta inserted posterior of reclinate seta; presutural supra-alar seta well developed, length greater than anterior notopleural seta; vein R_{4+5} basad of crossvein r-m lacking setulae; legs unicolorous, blackish brown . . . . . *Helaeomyia* Cresson

Genus *Actocetor* Becker

Actocetor Becker 1903: 169 [type species: *Ephydra margaritata* Wiedemann 1830 (= *Notiphila indica* Wiedemann 1824), by original designation]; 1926: 28–29 [review of Palearctic species].—Cresson 1929: 170–171 [discussion]; 1945: 66, 75 [distribution of species, key to genera]; 1946: 255–256 [review, Afrotropical fauna].—Wirth 1955: 51–53 [key to Afrotropical species].—Cogan 1980: 659 [Afrotropical catalog]; 1984: 139 [Palearctic catalog].—Mathis and Zatwarnicki 1995: 21–23 [world catalog].

Diagnosis.—Moderately small to medium-sized shore flies, body length 2.20–3.80 mm; head and thorax mostly yellowish with considerable whitish to cinereous microtomentum, abdomen reddish brown to black or dark blue (colors sometimes in combination), mostly bare, shiny.

Description.—*Head:* Insertion of antenna high on head, above dorsal ⅓ in lateral view; frons conspicuously wider than long; only reclinate fronto-orbital seta well developed; proclinate setae reduced, especially posterior seta, latter ½ of anterior seta; pseudopostocellar setae comparatively well developed, usually as large as larger proclinate fronto-orbital, mostly vertical, slightly to moderately divergent and reclinate; both inner and outer vertical setae present, well developed; vertex moderately creased; ocelli arranged in equilateral triangle, distance between posterior ocelli greater than between posterior ocellus and anterior ocellus; posterior ocelli situated immediately anterior to creased vertex. Antenna with 1st flagellomere short, length subequal to height of pedicel; scape not exerted; arista with 7–13 dorsal rays. Face densely invested with microtomentum, otherwise smooth, mostly flat, lacking pits or rugosity; usually 4 (sometimes 3 or 5) strong facial setae, inclinate, dorsalmost 1–2 setae large, cruciate. Eye appearing bare. Proboscis normally developed, not elongate.

Thorax: Generally yellow to pale brown or gray, with some cinereous microtomentum; supra-alar seta well developed, subequal or larger than postalar seta; acrostichal setae arranged in 6–8 irregular rows; prescutellar acrostichal setae present, well developed; postsutural supra-alar seta well developed; scutellum only slightly wider than long, disc densely setulose; basal scutellar seta over ½ length of apical seta; anepisternum with 1 large seta. Wing conspicuously maculate, guttate, generally dark with numerous white spots; subcostal break deeply incised; alula greatly reduced, a narrow band bearing setulae along posterior margin, or almost completely absent and lacking setulae; vein R_{2+3} extended normally to costal margin, lacking a subapical stump vein; vein R_{4+5} bearing 2–15 black setulae dorsally; halter whitish yellow to dark brown. Legs with forebasitarsus concolorous with remaining tarsomeres.

Abdomen: Generally bare of microtomentum, shiny, bronzish dark brown to black; 5th tergite bearing 4–8 well-developed, dorsally erect setae evenly spaced along posterior margin. Male terminalia (Figs. 31–38, 56–60): mostly symmetrical; epandrium generally thickly formed, U-shaped in posterior view, arms projected ventrad, well-developed erect setae along dorsum present or absent, numerous smaller setae present, lateral arms tapered gradually toward ventral apex; cercus in posterior view broadly oval, usually wider ventrally, dorsal apex more narrowly pointed; presurstylus (= surstylus) large, at ventral margin of epandrium, ventromedial surface with a small emargination; postsurstylus (= clasper) much longer than wide, bearing few to numerous setulae, especially apically, apex sometimes bilobed, bearing a postsurstylar process from basomedial surface, process medially and posteriorly directed, usually spatulate (often distinctly so); subepandrial plate broadly U-shaped, base longer than length of arms; aedeagus as a ring, sometimes angulate basally, and sometimes enlarged apically with phalanges that extend laterally or ventrally; aedeagal apodeme in lateral view more or less triangular, angle at attachment with hypandrium thicker; hypandrium bowl- or pouchlike, much narrower at articulation with aedeagal apodeme than with 5th sternite, becoming much wider toward anterior margin, concavity moderately deep.

Distribution.—Old World. Afrotropical (widespread), southern Palearctic (Canary Islands, Egypt, Israel, Oman, Spain, United Arab Emirates), and Oriental (widespread) regions.

Natural history.—The immature stages are unknown. Adults are often associated with sandy substrates, especially where there is highly organic matter, such as animal dung.

Variation.—A few species of *Actocetor* demonstrate variation in the degree and extent of microtomentum on abdominal tergites. The microtomentum usually forms transverse fascia toward the anterior and/or posterior margins and is usually more evident on the third and sometimes fourth tergites. Although most specimens have some microtomentum, there are occasional examples where none is evident or where the transverse fascia are very narrow and the microtomentum is sparse. Sometimes the overlap of the tergite immediately anterior partially obscures the fascia and artificially gives the impression of less or no microtomentum. The actual variation is expressed among conspecific specimens from the same locality and has led some workers to describe a species more than once.

As with microtomentum, the degree of coloration on the tergites can vary intraspecifically from yellow or more commonly yellowish red to metallic blackish blue. We suspect that the paler colored tergites correlate with more teneral specimens and that the dark, metallic color is characteristic of mature, fully sclerotized specimens.

We have used color of microtomentum on the scutellum and at the base of some thoracic setae as a character but caution against too much weight being given to these characters due to some variation. Although the extent of brown to blackish brown coloration is fairly dependable, this character varies and was not always entirely reliable.

Characters that were particularly reliable for diagnosing species were the pattern of wing spots and structures of the male terminalia, but even these demonstrated some variation. Variation in wing spots was mostly limited to size and shape rather than presence or absence. The shape of structures from the male terminalia varied far less. Of greater concern are slight changes in the aspect of a structure being observed and illustrated. These changes can easily give a false impression of variation and lead to misidentification.

Discussion.—*Actocetor* is one of the most easily recognized genera of shore flies, and we have discovered a number of synapomorphies that corroborate the monophyly of the genus. We have divided the corroborating characters into two groups: unambiguous synapomorphies and those with some homoplasy. The unambiguous characters are (parenthetic number as in discussion of characters and matrix): 1(1). 1st flagellomere short (length subequal to width of pedicel; an autapomorphy for *Actocetor*); 2(2). Position of antenna on head high, above dorsal ⅓ in lateral view (an autapomorphy for *Actocetor*); 3(7). Scutellum with apical ¼–¾ dark brown; 4(17). Vein R_{4+5} basad of crossvein r-m bearing 2 to several setulae. Characters showing some homoplasy are: 5(3). Pseudopostocellar setae well developed, as large as proclinate fronto-orbital seta (often or mostly slightly reclinate; a synapomorphy for *Actocetor, Eremomusca, Guttipsilopa,* and *Trypetomima*); 6(4). Face bearing 4 well-developed setae in a vertical row, dorsalmost 1–2 setae cruciate (a synapomorphy for *Actocetor* and *Guttipsilopa*); 7(9). Wing brown with white spots (a synapomorphy for *Actocetor, Guttipsilopa* (*Guttipsilopa*), and *Trypetomima*); 8(11). Alula reduced to a thin, bandlike lobe bearing numerous setulae (a synapomorphy for *Actocetor* (*Actocetor*) and genera *Eremomusca, Mimapsilopa,* and *Trypetomima*) or completely reduced and bearing no setulae (an autapomorphy for *Actocetor* (*Poecilostenia*); and 9(23). Setae on dorsum of epandrium well developed, dorsally erect (a synapomorphy for *Actocetor;* secondarily reduced in species of *Actocetor* (*Poecilostenia*).

We suggest that the genus *Trypetomima* is close to or is the sister group of *Actocetor,* primarily based on its similar wing pattern. *Trypetomima* differs from *Actocetor* in having a shortened vein R_{2+3} that bears a subapical stump vein. *Actocetor* is distinguished from *Trypetomima* by the characters noted in the diagnosis and by most of the characters listed as synapomorphies for this genus. Although we have suggested that *Trypetomima* is the sister group, we also included three other genera (*Guttipsilopa* (*Guttipsilopa*), *Eremomusca,* and *Mimapsilopa*) as outgroups in the phylogenetic analysis.

Narrowing of the wing in *Actocetor* has occurred independently at least twice, in *A. afrus* of the subgenus *Actocetor* and in species of the subgenus *Poecilostenia.* The narrowing in species of *Poecilostenia* is more radical than in *A. afrus,* and the condition in the latter species is somewhat intermediate between *Poecilostenia* and other species of the subgenus *Actocetor* (details more specifically documented under *A. afrus* and *Poecilostenia*). We do not know the basis or any adaptive advantage for narrowing of the wing. Although flight is apparently still possible with the narrowed wing, that condition may affect its efficiency.

KEY TO SPECIES OF *ACTOCETOR*

1. Setulae on vein R_{4+5} basad and apicad of crossvein r-m; vein CuA_1 conspicuously sinuous along posterior margin of discal cell; discal cell with at most 1 white spot (subgenus *Poecilostenia*; Afrotropical) 5
– Setulae on vein R_{4+5} only basad of crossvein r-m; vein CuA_1 nearly straight along posterior margin of discal cell; discal cell with 2–3 white spots (subgenus *Actocetor*) 2
2. Cell r_1 with only 1 sub-basal white spot 4
– Cell r_1 with 2 white spots, 1 sub-basal spot and 1 subapical spot 3
3. Discal cell with 2 white spots (sub-basal spot broadly U-shaped; subapical spot often constricted medially, sometimes forming anterior and posterior spots); cell CuA_1 normally developed, broader than discal cell; basal half of cell CuA_1 white; base of 4th tergite generally with broad anterior band of gray microtomentum (sometimes thin lateral bands on 3rd and 5th tergites present or no microtomentum at all) (Afrotropical: widespread; Oriental: India, Malaysia, Sri Lanka; southern Palearctic: Canary Islands, Egypt, Israel, Oman, Spain, United Arab Emirates) . . . . *A. indicus* (Wiedemann)
– Discal cell with 3 white spots; cell CuA_1 narrower than discal cell, anal margin nearly straight; 1 white spot present in basal half of cell CuA_1; tergites 3–5 with broad bands of gray microtomentum basally (Afrotropical: Liberia, Senegal) . . . . *A. afrus,* new species
4. Cell r_{4+5} with 2 white spots; vein R_{4+5} bearing 2–4 setulae basad of crossvein r-m (Afrotropical: Madagascar) . . . . . *A. hovus* Giordani Soika
– Cell r_{4+5} with 3 white spots (sub-basal spot often small); vein R_{4+5} bearing 5–6 setulae basad of crossvein r-m (Oriental: widespread) . . . . *A. nigrifinis* (Walker)
5. Cell r_1 with 2 white spots, 1 sub-basal spot and 1 medial spot; discal cell without spots but with an apical, crescent-shaped, paler bulla; abdomen mostly microtomentose, tergites 3–7 entirely gray and brown microtomentose (Tanzania) . . . . *A. lindneri* Wirth
– Cell r_1 with only 1 medial, white spot; discal cell spots variable but without an apical bulla; abdomen mostly shiny, only tergites 3–4 with thin gray microtomentose, anterior bands . . . 6
6. Discal cell with 1 medial, white spot; scutellum with apical ½–¾ dark brown (widespread) . . . . *A. decemguttatus* (Bezzi)
– Discal cell without a white spot; scutellum entirely concolorous with yellowish to slightly brownish yellow scutum (Ethiopia) . . . . *A. yaromi,* new species

Subgenus *Actocetor* Becker

Actocetor Becker 1903: 169 [as a genus; type species: *Ephydra margaritata* Wiedemann 1830 (= *Notiphila indica* Wiedemann 1824), original designation].—Wirth 1955: 51 [key].

Diagnosis.—This subgenus is distinguished from the subgenus *Poecilostenia* by the following combination of characters:

Description.—*Thorax:* Mesonotum generally gray to brownish gray microtomentose. Wing alula greatly reduced, thin and bandlike, lobe bearing numerous short to long setulae along posterior margin; anal angle of wing moderately well developed, cell cua_1 much broader or narrower than discal cell; vein CuA_1 nearly straight along posterior margin of discal cell; dorsal surface of vein R_{4+5} bearing 2–6 setulae, only basad of crossvein r-m; discal cell with 2–3 white spots. Knob of halter variously shaped, white to brown.

Abdomen: 5th tergite of male bearing 6–8 well-developed setae along posterior margin; epandrium bearing 4–8 well-developed setae transversely along dorsum; aedeagus basally an angulate, well-sclerotized ring, apical ⅓–½ enlarged in some species as lateral or ventral phalanges; aedeagal apodeme simple, lacking a distinct keel; hypandrium simple, pouch like, narrowed at attachment with aedeagal apodeme, much wider at attachment with 5th sternite.

Discussion.—Specimens of this subgenus are relatively common in collections, and long series from a single locality were typically available, making assessment of variation more convenient and reliable. In addition to being relatively common, two species, *A. indicus* and *A. nigrifinis,* are widespread. The former occurs throughout the Oriental Region and the latter is found throughout Africa with extensions into the Indian Subcontinent and Malaysia as well as into the southern Palearctic Region (Spain, United Arab Emirates). The records from the Indian Subcontinent, the Seychelles, and Malaysia are occurrences in disjunct areas, and as such they may also represent introductions. Sampling error may also be a factor in the apparent disjunctions. A third species of this subgenus, *A. hovus,* is endemic to Madagascar and is the only species of *Actocetor* known from that island, and the fourth species, *A. afrus,* occurs in West Africa (Liberia and Senegal).

The subgenus *Actocetor* is monophyletic, as indicated on the cladogram (Fig. 65) and as substantiated by the following characters (characters marked with an * are unambiguous): 8*. Color surrounding base of prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae distinctly dark brown; 15*. Discal cell with two white spots; 23*. Dorsum of epandrium bearing well-developed, dorsally erect setae; 25*. Male 5th sternite trapezoidal, divided medially into two sclerites; 26. Postsurstylar process present, expanded ventrally and projected to a point posteriorly (secondarily modified in *A. indicus* and *A. nigrifinis*); 28. Presurstylus bearing one round to oval lobe medially (secondarily modified in *A. indicus* and *A. hovus*).

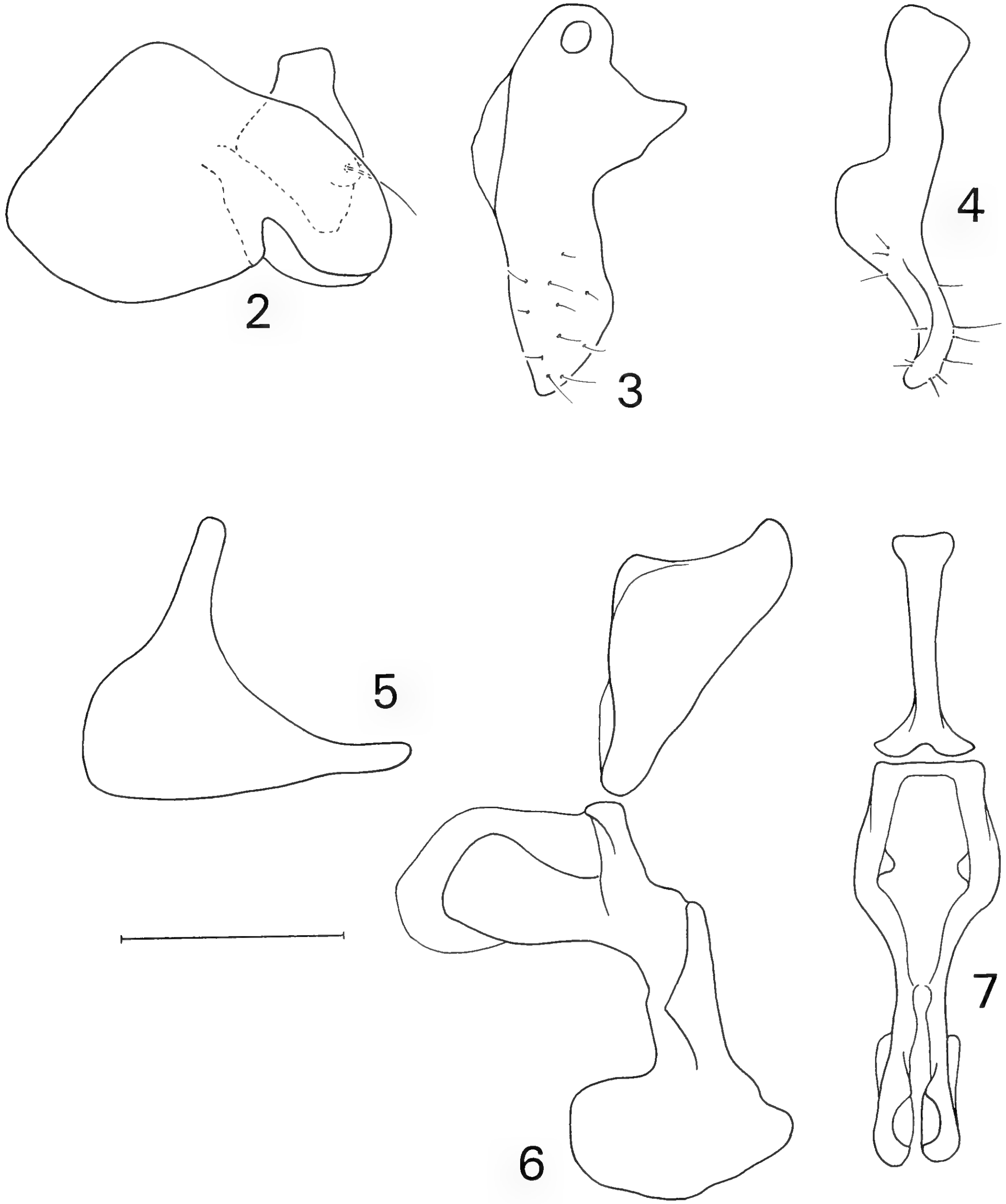
Actocetor (*Actocetor*) *afrus* Dikow and Mathis, new species

(Figs. 2–7, 51)

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.10–3.10 mm.

Description.—*Head:* Arista with 9–12 dorsal rays. Gena-to-eye ratio 0.25–0.28.

Thorax: Mesonotum densely microtomentose, tannish gray to whitish gray, pleura whitish to silvery gray; 2 brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, basal scutellar setae) dark brown; scutellum with apical ⅓–¼ brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 51) very narrow, cell cua_1 narrower than discal cell, anal margin nearly straight;



Figs. 2–7. Structures of the male terminalia of *Actocetor afrus*. 2, Presurstylus, posterior view. 3, Postsurstylus, lateral view. 4, Same, posterior view. 5, Postsurstylar process, posterior view. 6, Aedeagus, aedeagal apodeme, dorsal view. 7, Same, lateral view. Scale bar equals 0.1 mm.

alula narrow, bandlike, bearing short setulae (length of setulae equal to height of alula) along posterior margin; vein R_{4+5} bearing 5 setulae basad of crossvein r-m; wing pattern as follows: cell c with basal half white; cell r_1 with transversely rectangular to trapezoidal, basal spot, and oval-rectangular subapical spot; cell r_{2+3} with 2 spots, basal rectangular/trapezoidal spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a circular medial spot in line with apical spot in cell r_{2+3}, and an apical spot; discal cell with 3 circular spot, sub-basal, medial, and subapical; cell m with transversely oval/rectangular spot; cell cua_1 with 2 spots, rectangular sub-basal spot, and transversely trapezoidal subapical spot, vein CuA_1 straight between these spots; costal vein ratio 0.80–0.89; M vein ratio 1.05–1.15. Halter stem yellowish white basally, apical part of stem and knob tan to brown; knob only slightly expanded from diameter of stem, not distinctly clavate. Legs generally whitish yellow to yellow.

Abdomen: Base of 1st tergite with thin band of gray microtomentum; bases of tergites 3–5 with broad bands of gray microtomentum, otherwise tergites bronzish dark brown to metallic black. Male 5th sternite trapezoidal, bearing numerous setulae that are more or less evenly scattered over surface, sternite divided medially along entire length, forming 2 sclerites. Male terminalia (Figs. 2–7): presurstylus large, ventromedial surface with a small emargination, bearing 1 medial lobe along ventral margin; postsurstylus (Fig. 3) much longer than wide, bearing 9–11 scattered setulae on both surfaces, with more setulae apically, apex tapered, pointed to one side, not bilobed; postsurstylar process distinctly footlike (Fig. 5), apical enlargement bluntly pointed posteriorly and rounded anteriorly; aedeagus (Fig. 6) as a subrectangular ring basally with a very large lateral phalange that extends ventrally; aedeagal apodeme (Fig. 6) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, broader toward attachment with aedeagal apodeme; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type Material.—The holotype ♂ is labeled "SENEGAL; 3 KM SSE BRIN, 11 KM SW ZIGUINCHOR. 9.XI.1977 [9 Nov 1977] UTM 28PCJ53-83. LOC.NO.22/ LUND UNIV. SYST. DEPT. SWEDEN-GAMBIA/SENEGAL NOV 1977-CEDERHOLM-DANIELSSON-HAMMARSTEDT-HEDQVIST-SAMUELSSON/margaritatus Wied. det. Canzoneri S. ["margaritatus Wied." handwritten]/HOLOTYPE ♂ Actocetor afrus Dikow & W.N. Mathis [red; species' name and gender and "Dikow &" handwritten]. The holotype is double mounted (minuten in a plastic rectangle), is in fair condition (several setae misoriented, thorax cracked, wings with tears and apices missing), and is deposited in the ZIL. Paratypes, 1 ♂ and 1 ♀, bear the same locality label as the holotype and are deposited in the BMNH.

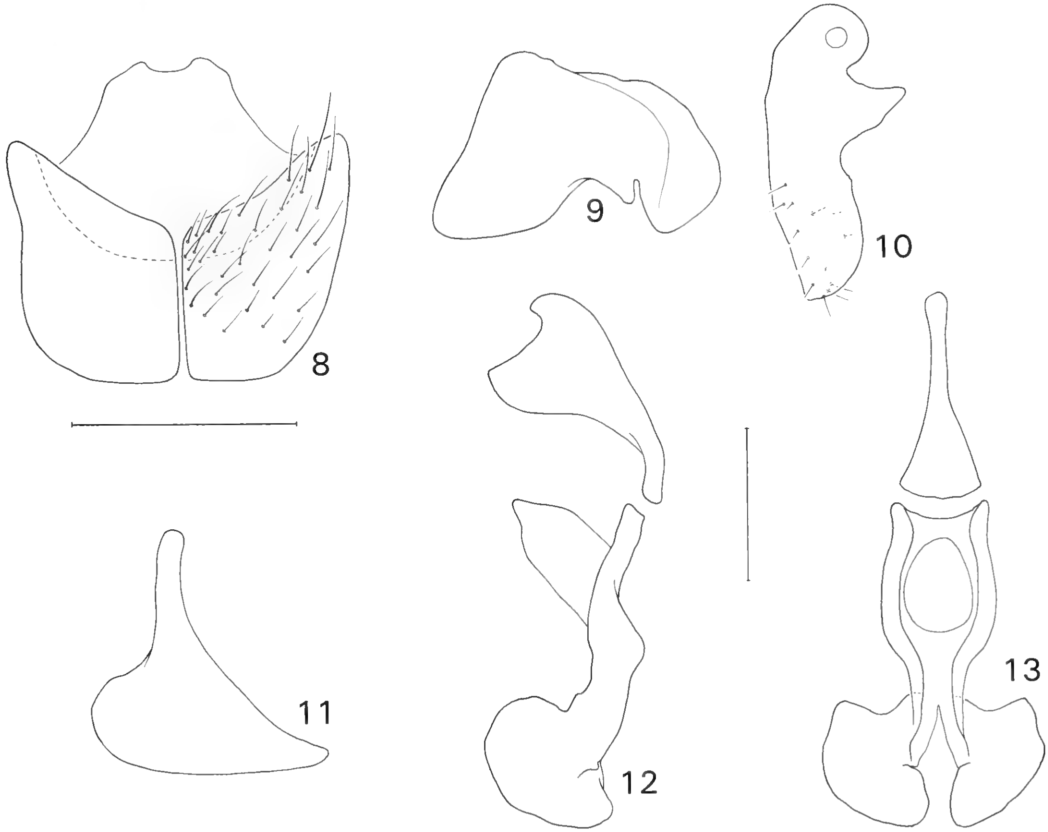
Other specimen examined.—AFROTROPICAL. LIBERIA. Genewonday (roadside), 17 Feb 1953, C. Blickenstaff (1♀; USNM).

Distribution.—Afrotropical: Liberia and Senegal.

Etymology.—The species epithet, *afrus,* denotes the continent where this species occurs.

Remarks.—This species is somewhat intermediate in many morphological features between the two subgenera. The epandrium, for example, is typical of the subgenus *Actocetor,* bearing large setae along the dorsum, and other characters of the male terminalia are also typical of *Actocetor* sensu stricto. The narrow wing (Fig. 51), however, is somewhat intermediate, being narrower than other species of *Actocetor* sensu stricto but not quite as narrow as species of *Poecilostenia.* The alula is narrow and bandlike, and bears some short setulae along the posterior margin, somewhat like *Actocetor* sensu stricto. The anal lobe, however, is narrower and straighter than *Actocetor* sensu stricto but not as narrow and straight as *Poecilostenia.*

The structures of the male terminalia are very similar to those of *A. hovus,* and based on these features alone, we would have sug-



Figs. 8–13. Structures of the male preabdomen and terminalia of *Actocetor hovus*. 8, Fifth sternite and hypandrium, ventral view (only left side showing setae). 9, Presurstylus, posterior view. 10, Postsurstylus, lateral view. 11, Postsurstylar process, posterior view. 12, Aedeagus and aedeagal apodeme, lateral view. 13, Same, dorsal view. Scale bar equals 0.3 mm for Fig. 8 and 0.1 mm for Figs. 9–13.

gested this species was closely related to *A. hovus*. The wings of these species are significantly and consistently different from each other, and the wing characters, coupled with the disjunct distribution, are the basis for recognizing this species as distinct.

Actocetor (*Actocetor*) *hovus* Giordani Soika
(Figs. 8–14, 48)

Actocetor hova Giordani Soika 1956a: 126.—Cogan, 1980: 659 [Afrotropical catalog].—Mathis and Zatwarnicki 1995: 22 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.70–3.20 mm.

Description.—*Head:* Arista with 7–11 dorsal rays. Gena high, higher than height of pedicel, gena-to-eye ratio 0.29–0.31.

Thorax: Mesonotum densely microtomentose, tannish gray to whitish gray, pleura whitish to silvery gray; 2 short, dark brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, basal scutellar setae) dark brown; scutellum with apical ½–¾ dark brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 48) normally developed with wide anal angle; alula narrow, bandlike, bearing long setulae (length twice height of alula) along posterior margin; vein R_{4+5} bearing 2–4 setae basad of crossvein r-m; wing pattern as follows: cell c with only a pale spot (not as transparent as other spots); cell r_1 with 1 sub-basal, subrectangular spot; cell r_{2+3} with 2 spots, basal spot in line with spot in cell r_1, apical spot, transversely oval/rectangular, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a medial spot, in line with crossvein dm-cu, and an apical spot; discal cell with a wide, U-shaped, basal spot (apical arm sometimes constricted) and a subapical, transversely rectangular spot; cell m with a transversely oval spot near middle; cell cua_1 with basal ⅓ white and a subapical spot, vein CuA_1 straight; costal vein ratio 0.73–0.85; M vein ratio 0.89–0.98. Knob of halter yellowish brown to brown and distinctly clubbed. Legs generally whitish yellow to yellow; forecoxa and base of femora sometimes with whitish gray to gray microtomentum.

Abdomen: Entirely shiny, only base of 1st tergite with gray microtomentum; generally metallic, dark blue, often totally dark blue but sometimes yellow to yellowish red at anterior and/or posterior margins. Male 5th sternite trapezoidal (Fig. 8), bearing numerous setulae that are more or less evenly scattered over surface, sternite divided medially along entire length, making 2 plates. Male terminalia (Figs. 9–13): presurstylus (Fig. 9) large, ventromedial surface with a small emargination, bearing 2 lobes along ventral margin, medial lobe much larger, 1 smaller, thumblike process between medial lobe and expanded base; postsurstylus (Fig. 10) much longer than wide, bearing 7–8 scattered setulae on both surfaces, with more setulae apically, apex bluntly formed and not bilobed; postsurstylar process (Fig. 11) distinctly footlike, apical enlargement pointed posteriorly and rounded anteriorly; aedeagus (Fig. 12) as a subrectangular ring basally with a very large lateral phalange that extends laterally; aedeagal apodeme (Fig. 12) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, broader toward attachment with aedeagal apodeme; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type material.—The holotype ♂ of *Actocetor hovus* is labeled "HOLOTYPUS [orange; black submargin]/COLL. MUS. CONGO Madagascar: Maroansetra XII-1949 [Dec 1949] J. Vadon/det. Giordani Soika 1957 [handwritten]/Actocetor hova [handwritten; red]." The holotype is double mounted (minuten in a block of polyporus), is in good condition, and is deposited in the MRAC.

Other specimens examined.—AFROTROPICAL. MADAGASCAR. *Antseranana:* Nosy Bé beach, Ambatoloaka, 4–7 Apr 1991, A. Freidberg, F. Kaplan (1♂; USNM); Nosy Tanikely, 6 Apr 1991, A. Freidberg, F. Kaplan (1♀; USNM). *Fianarantsoa:* Ranomafana (21°15′S, 47°27′E; 600 m; on sunlit sand bar at river margin, montane rain forest), 29 Aug 1993, W. E. Steiner (2♀; USNM). *Toamasina:* Maroantsetra, Dec 1949, J. Vadon (1♂ holotype, MRAC; 1♀ paratype, USNM); Perinet, Dec 1955, B. Stuckenberg (1♂, 1♀; NMSA). *Toliara:* Fenerive (coastal forest), Dec 1955, B. Stuckenberg (1♂; NMSA); Ranohira (860 m), 26 Jan–4 Feb 1958, B. Stuckenberg (1♂; NMSA); Sud-Est Sainte Luce, Fort Dauphin (= Taolanaro; 10 m), 22–24 Feb 1953, B. Stuckenberg (1♀; NMSA).

Distribution (Fig. 14).—Afrotropical: Madagascar (Antseranana, Fianarantsoa, Toamasina, Toliara).

Remarks.—Variation is evident in the coloration of the abdomen and to a lesser degree in the size of the white spots in the wing. The abdomen is often entirely dark, metallic blue, but many specimens have some yellow to yellowish red color on the basal tergites, usually toward either the anterior or posterior margins.

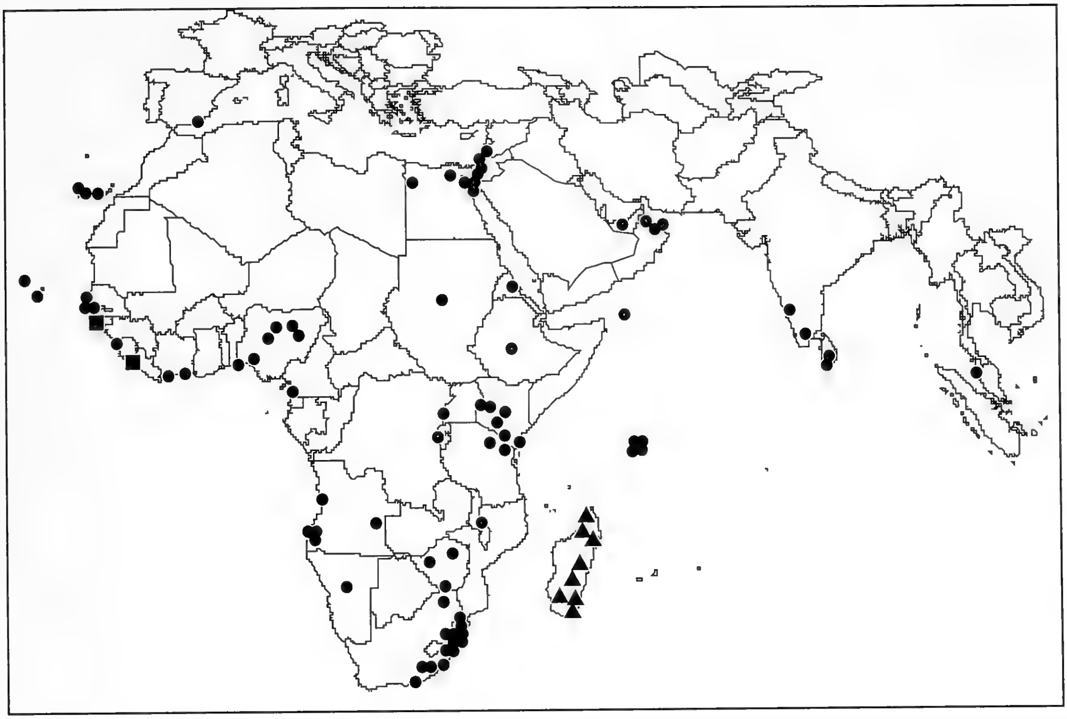


Fig. 14. Distribution map for *Actocetor afrus* (filled squares), *A. hovus* (filled triangles), and *A. indicus* (filled circles).

Actocetor (*Actocetor*) *indicus* (Wiedemann)
(Figs. 1, 14–38, 49)

Notiphila indica Wiedemann 1824: 58.

Actocetor indicus: Cogan and Wirth 1977: 328 [generic combination].—Mathis and Zatwarnicki 1995: 22 [world catalog].

Ephydra margaritata Wiedemann 1830: 594. **New synonym.**

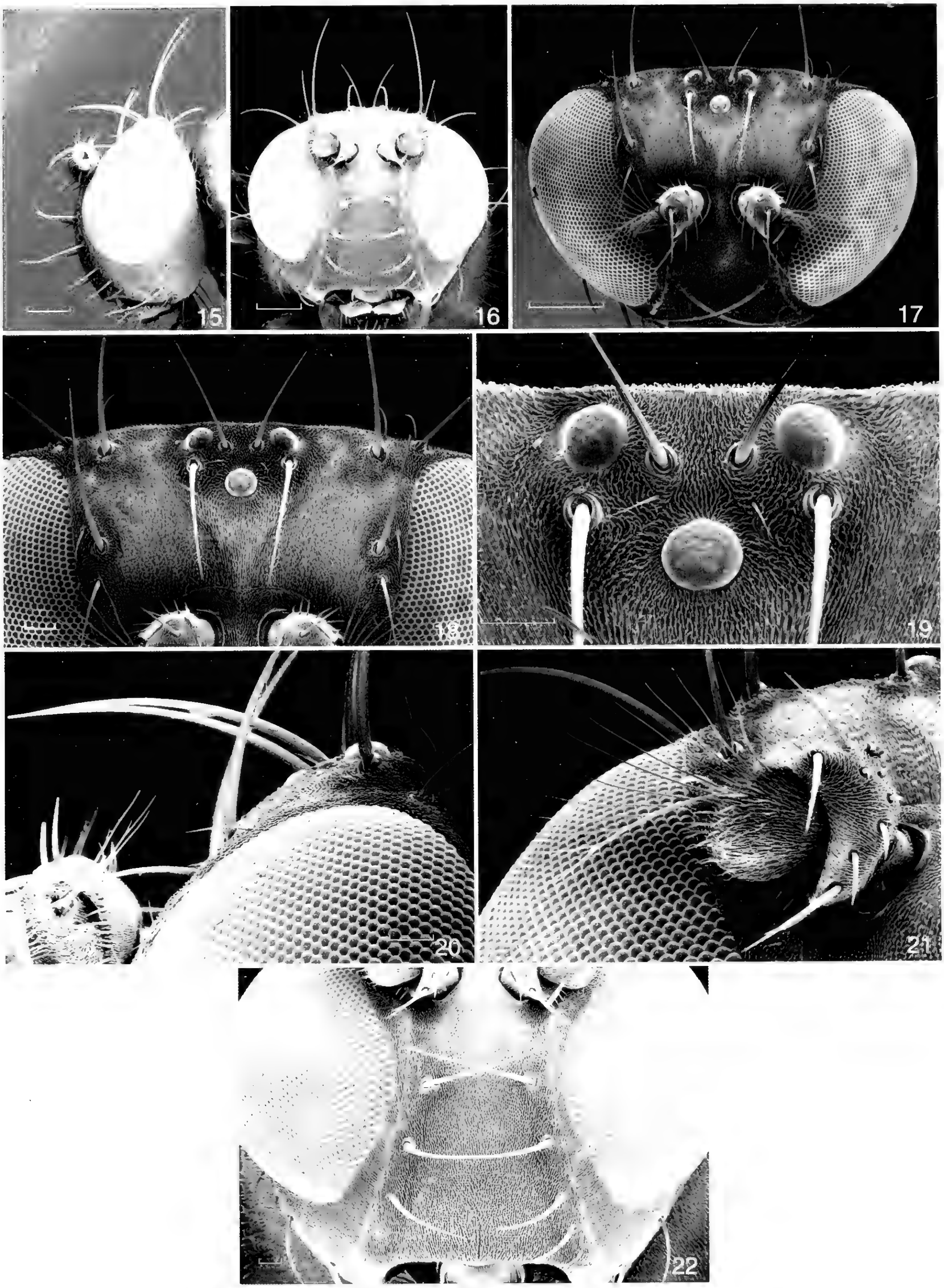
Actocetor margaritatus: Becker 1903: 170 [generic combination].—Cresson 1929: 171 [review]; 1945: 66 [list, India]; 1946: 255 [review, list, Sudan, Zimbabwe].—Séguy 1953: 86 [list].—Wirth 1955: 52 [review].—Giordani Soika 1956b: 106–107 [review, distribution]; 1956c: 503 [review, list, Rwanda].—Frey 1958a: 54 [list, Canary Islands].—Stower et al. 1958: 27 [scavenger in egg pods of desert locusts].—Greathead 1963: 452 [reared from damaged egg pods of desert locusts].—Cogan 1980: 659 [Afrotropical catalog].—Rossi 1988: 174–175 [parasite: *Stigmatomyces rampinii* Rossi (Laboulbeniaceae)].—Mathis and Zatwarnicki 1995: 22 [world catalog].—Canzoneri and Rampini 1996: 12 [list, Sierra Leone].

Actocetor beckeri Hendel 1917: 41 [preoccupied].—Cresson 1946: 255–256 [list].

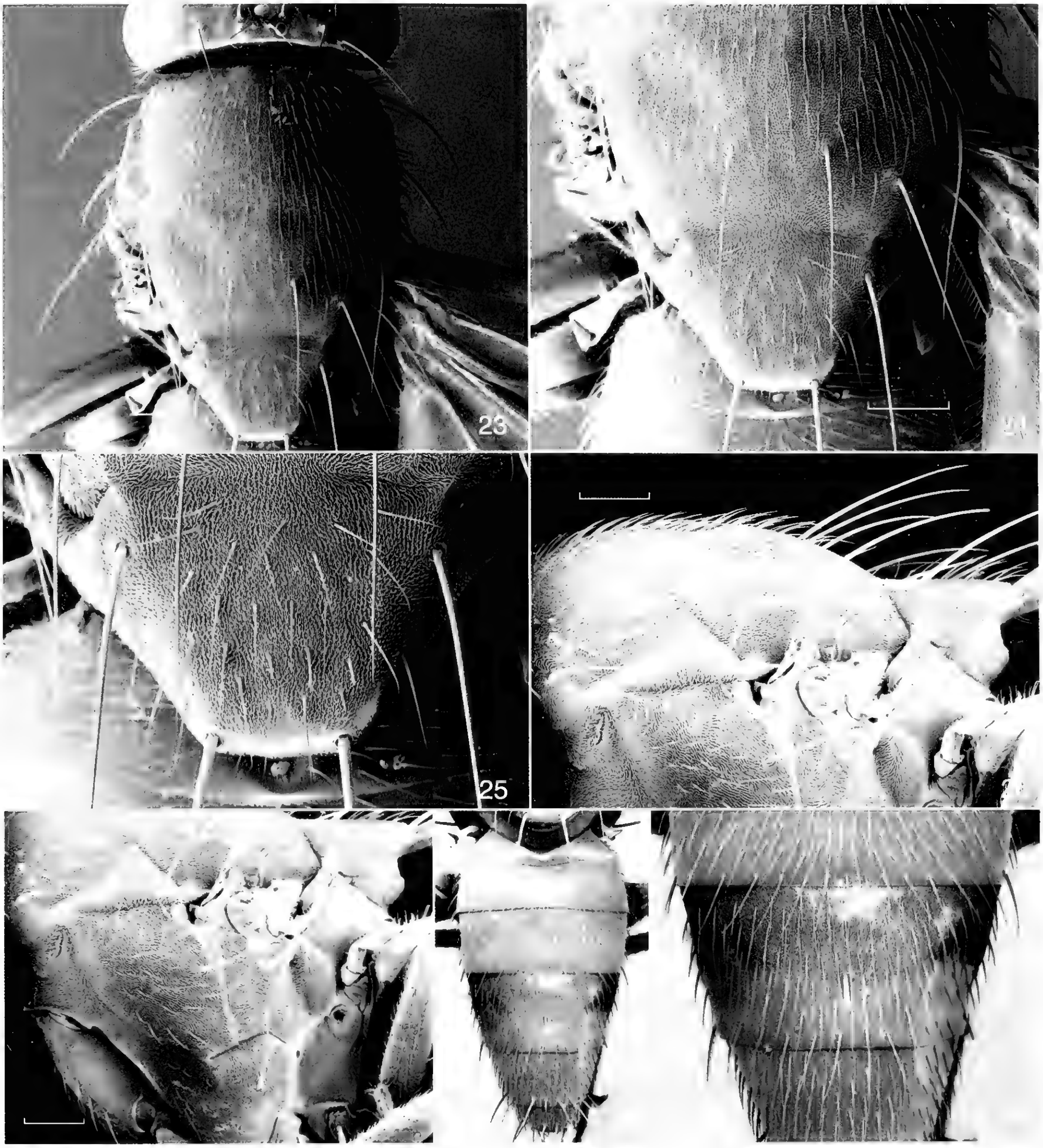
Actocetor hendeli de Meijere 1924: 202 [replacement name for *Actocetor beckeri* Hendel 1917, not de Meijere 1916].—Cresson 1946: 255–256 [discussion, probably a variety of *A. margaritatus*].—Cogan 1980: 659 [Afrotropical catalog].—Mathis and Zatwarnicki 1995: 22 [world catalog]. **New synonym.**

Actocetor margaritatus panelii Frey 1958b: 46 [Cape Verde Islands. São Vincente: Rib. Juliao. Boa Vista: Rabil. São Tiago: Rib. Charco; ST ♂♀, MZH].—Cogan, 1980: 659 [Afrotropical catalog]. **New synonym.**

Actocetor panelii: Mathis and Zatwarnicki 1995: 22 [revised status].



Figs. 15–22. Scanning electron micrographs of *Actocetor indicus*. 15, Head, lateral view (scale = 0.2 mm). 16, Same, anterior view (scale = 0.2 mm). 17, Same, anterodorsal view (scale = 0.2 mm). 18, Frons, anterodorsal view (scale = 50 μm). 19, Ocellar triangle, anterodorsal view (scale = 50 μm). 20, Dorsum of head, lateral view (scale = 50 μm). 21, Left antenna, anterolateral view (scale = 50 μm). 22, Face, anterior view (scale = 50 μm).



Figs. 23–29. Scanning electron micrographs of *Actocetor indicus.* 23, Mesonotum, dorsal view (scale = 0.2 mm). 24, Posterior portion of scutum and scutellum, dorsal view (scale = 0.2 mm). 25, Scutellum, dorsal view (scale = 50 μm). 26, Dorsum of mesonotum, lateral view (scale = 0.2 mm). 27, Pleura, lateral view (scale = 0.2 mm). 28, Abdomen, dorsal view (scale = 0.2 mm). 29, Abdominal tergites 3, 4, and 5, dorsal view (scale = 0.2 mm).

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.20–3.80 mm; habitus as in Fig. 1.

Description.—*Head* (Figs. 15–22): Arista with 9–12 dorsal rays. Gena high, higher than height of pedicel, gena-to-eye ratio 0.21–0.36.

Thorax (Figs. 23–27, 49): Mesonotum densely microtomentose, tannish gray to whitish gray, pleura whitish to silvery gray;

2 more or less short, dark brown bars may be present anteriorly, separated by gap equal to distance between prescutellar acrostichal setae (sometimes fused posteromedially, mesonotum in these specimens pale brown); rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae) usually not dark brown; scutellum with apical ¼–⅓ dark brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 49) normally developed with wide anal angle; alula narrow, bandlike, bearing long setulae (length twice height of alula) along posterior margin; vein R_{4+5} bearing 5–6 setae basad of crossvein r-m; wing pattern as follows: cell c with basal ½ white; cell r_1 with 2 spots, 1 sub-basal, subrectangular spot and 1 subapical rectangular to trapezoidal spot; cell r_{2+3} with 2 spots, basal spot in line with spot in cell r_1, apical spot, transversely oval/rectangular, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with subcircular, medial spot, in line with crossvein dm-cu, and an apical spot (some specimens with a trace of a 3rd sub-basal spot); discal cell with a wide, U-shaped, basal spot (apical arm sometimes constricted) and a subapical, transversely oval-rectangular spot, sometimes divided into 2 circular spots; cell m with a transversely oval-rectangular spot near middle; cell cua_1 with a large, basal rectangular white and a subapical, transversely trapezoidal spot, vein CuA_1 straight; costal vein ratio 0.54–0.72; M vein ratio 0.84–1.0. Halter stem yellow; knob whitish yellow and distinctly clubbed. Legs generally whitish yellow to yellow; forecoxa and base of femora sometimes with whitish gray to gray microtomentum laterally.

Abdomen (Fig. 28–38): Mostly shiny, gray microtomentum almost always present and as follows: base of 1st tergite with thin band; 4th tergite with wide, anterior band; sometimes with thin, lateral bands on 3rd and 5th tergites or with medial spot on 3rd tergite; color generally metallic, dark blue to black, often with yellow to yellowish red at anterior and/or posterior margins or sometimes entirely yellowish red. 3rd and 4th sternites rectangular, broad, 1–2× longer than wide; 5th sternite of male (Fig. 30) trapezoidal with medial weakness or slight indentation on concave posterior margin. Male terminalia (Figs. 31–38): epandrium (Figs. 31–32) higher than wide; presurstylus (Fig. 33) large, ventromedial surface with a small emargination, bearing 2 round to oval lobes medially; postsurstylus (Fig. 34) much longer than wide, bearing 3–4, apical setulae, apex bilobed with a small, digitiform, medial, pointed process; postsurstylar process (Fig. 35) distinctly spatulate, rounded process, shaped like an halter; aedeagus (Fig. 37) as a subrectangular ring basally from which a lateral phalange extends apically; aedeagal apodeme (Fig. 38) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, broader toward attachment with aedeagal apodeme; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type material.—The lectotype ♀ of *Notiphila indica* Wiedemann, here designated to stabilize and make more universal the use of this name, is labeled "TYPE [red]/ Notiphila indica Wied. Ind[ia]. orient. [handwritten]/Notiphila indica Wied. Det. B.H. Cogan 1976. [species name and "76" handwritten]/Actocetor indicus (Wied.) Det. B.H. Cogan 1976. [species name and "76" handwritten]/LECTOTYPE ♀ Notiphila indica Wiedemann By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is directly pinned, is in fair condition (the specimen is greasy and the pin bears some verdigris), and is deposited in the UZMC.

The lectotype ♀ of *Ephydra margaritata* Wiedemann, here designated to stabilize and make more universal the use of this name, is labeled "[a small pink square]/ Egypten [handwritten]/margaritata [handwritten] Coll. Winth. [black margin along longer sides of label]/Ephydra margaritata W Aegyptn. [handwritten]/Type [red]/LECTOTYPE ♀ Ephydra margaritata Wiedemann By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is pinned directly, is in fair condition (several setae missing), and is deposited in the NMW. A ♂, presumably a syntype, is labeled "Egypten [handwritten]/margaritata [handwritten] Coll. Winth./margaritata W Egyptn [handwritten]." and is deposited in the NMW.

A ♂ paratype of *Actocetor margaritatus panelii* Frey from the type locality was examined, including structures of the dissected male terminalia.

The holotype ♂ of *Actocetor beckeri* Hendel (replaced with *A. hendeli* by de Meijere) is labeled "Algoa bay Capland 22 3 96 [22 Mar 1896; handwritten] Dr. Brauns./Actocetor Beckeri, n. sp. [2 black submarginal borders; handwritten]/violaceus nom. nov. det. Hendel [all except "det. Hendel" handwritten]/Coll. Hendel/HOLOTYPE ♂ Actocetor beckeri Hendel [red submarginal border; species name, author, and gender handwritten]". The holotype is double mounted (minuten in a cardboard card), is in poor condition (both wings are missing and several setae are broken), and is deposited in the NMW.

Other specimens examined.—AFROTROPICAL. ANGOLA. Bruco, 26 Feb–2 Mar 1972 (4♂, 4♀; BMNH); Cachoeiras (20 mi SW Gabela), 18–19 Mar 1972 (1♀; BMNH); Rio Curoca (7 mi N Rio Alexandre), 25–26 Feb 1972 (2♂, 2♀; BMNH); Rio Giraul (10 mi NE Mocamedes), 27–29 Feb 1972 (1♀; BMNH); Santa Clara, 19 Mar 1972 (1♀; BMNH); Tundavala (8 mi NW Sa da Bandeira), 27–29 Mar 1972 (1♀; BMNH).

BOTSWANA. River Semowane, 23–24 Apr 1972 (1♂, 1♀; BMNH).

CAMEROON. Kribi (Rt. N7; beach), 28–29 Nov 1987, A. Freidberg (2♀; USNM).

CAPE VERDE ISLANDS. São Vincente: Rib. Juliao, 26 Nov–2 Dec 1953, Lindberg (1♂; USNM). São Jorge dos Orgãos (alfalfa field), Jun 1986, A. van Harten (3♂, 1♀; NMWL).

DEMOCRATIC REPUBLIC OF CONGO. Rumonge (Urundi), 1932, A. Lestrade (1♀; MRAC).

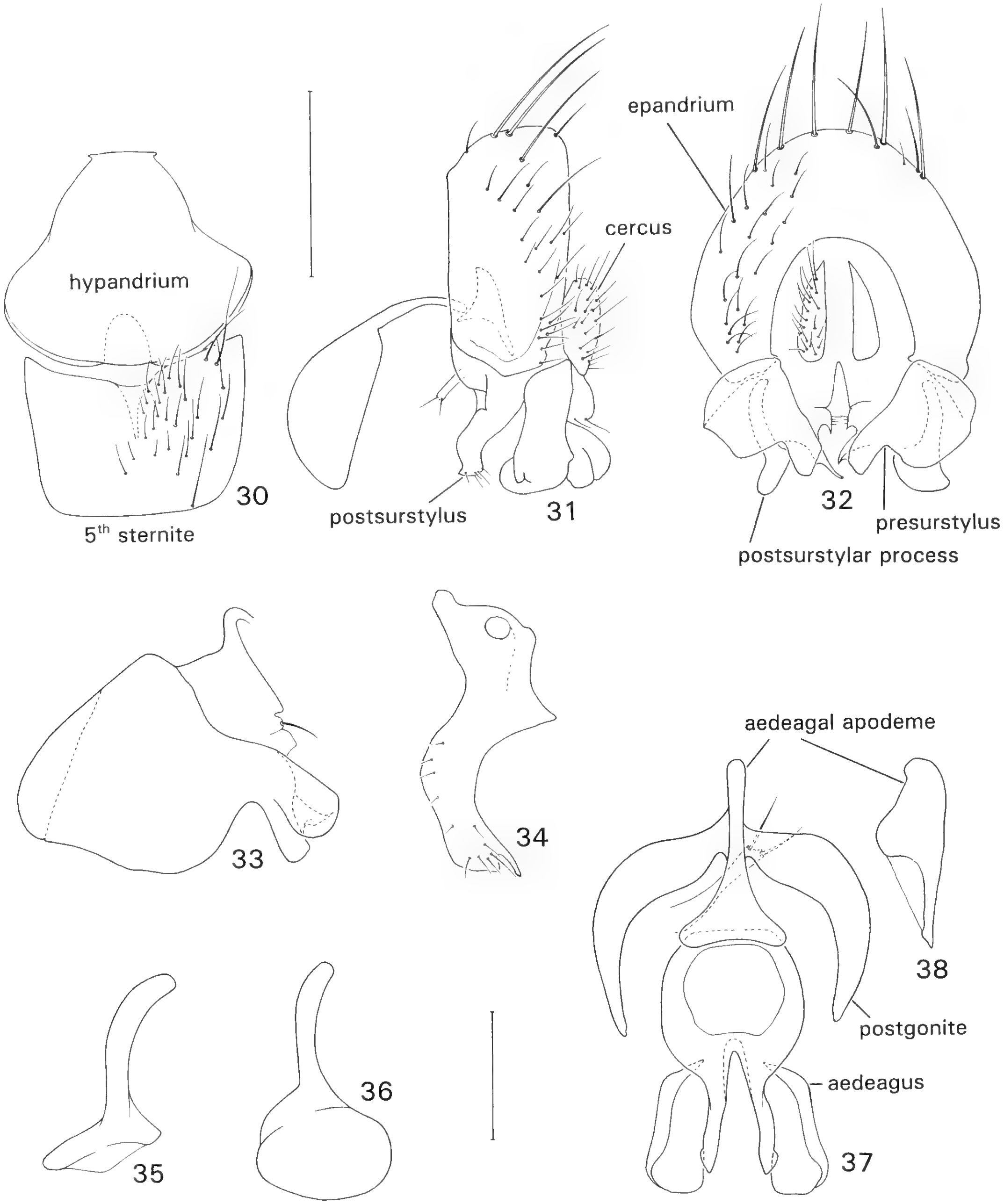
ERITREA. Ailet (from egg-pods), 22 Jul 1956, D. J. Greathead (3♂, 1♀; BMNH); Massawa (15 mi N, from egg-pods emerged), 20 Mar 1954, Natural Resources Institute Coll (1♂, 1♀; BMNH).

ETHIOPIA. Lake Langano, 13 Dec 1989, A. Freidberg, F. Kaplan (1♂; USNM).

GAMBIA. Bakau, Cape St. Mary (at Sun Wing Hotel, swept in vegetation along beach), 5 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♂, 2♀; BMNH, ZIL); Bakau at Tropic Bungalow (swept in meadow, rich in flowers, at beach), 4 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♂; BMNH); Jul–Sep 1927 (on ground-nut plots) (1♂; BMNH). Central Banjol (3 km NW; garden), 21 Feb 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♀; ZIL). Central Banjol (3 km NW; in vegetation along mangrove), 21–22 Feb 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♀; ZIL). Kotu Stream (3 km SW Bakau; in vegetation), 23 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (2♀; ZIL).

IVORY COAST. Abidjan, Riviera near Golf Club (05°10′N, 04°00′W; scrubland near edge Ebrie lagoon), 21 Apr 1989, J. G. H. Londt (1♂, 4♀; NMSA). Banco National Park, N Abidjan (05°22′N, 04°03′W; edge of wide track in forest), 23–27 Apr 1989, J. G. H. Londt (1♂; NMSA). Fresco (15 km W; 05°06′N, 05°43′W; airfield/forest edge, near Palmindustrie), 24 Apr 1989, J. G. H. Londt (1♂; NMSA).

KENYA. Biretwo (40 km E Eldoret), 12 May 1991, A. Freidberg, F. Kaplan (1♀;



Figs. 30–38. Structures of the male preabdomen and terminalia of *Actocetor indicus*. 30, Fifth sternite and hypandrium, ventral view (only left side showing setae). 31, Epandrium, cerci, presurstylus, postsurstylus, gonite, and hypandrium, lateral view. 32, Same, posterior view. 33, Presurstylus, posterior view. 34, Postsurstylus, lateral view. 35, Postsurstylar process, posterior view. 36, Same, posteroventral view. 37, Aedeagus, aedeagal apodeme, dorsal view. 38, Aedeagal apodeme, lateral view. Scale bar equals 0.3 mm for Figs. 30–32 and 0.1 mm for Figs. 33–38.

USNM). Bungoma, 6–7 Nov 1983, A. Freidberg (1♀; USNM). Isolo (5 km S), 30 Nov 1986, A. Freidberg (1♀; TAU). Mombasa (beach) 5 Dec 1989, A. Freidberg, F. Kaplan (2♀; TAU, USNM). Mombasa (10 km N), 18 Aug 1996, A. Freidberg (1♂; USNM). Mombasa (20 mi S; Malaise trap), 23–25 Jan 1968, K. V. Krombein, P. J. Spangler (1♀; USNM). Nairobi (50 km SE; Rt. A109), 30 Apr 1991, A. Freidberg, F. Kaplan (1♀; TAU). Rift Valley, Ol Arabe Gorge, 11 Nov 1988, R. K. Butlin (1♂, 1♀; NMWL). Tsavo West, Ngulia Lodge, 16–17 Aug 1983, A. Freidberg (1♂, 3♀; USNM). Tseikuru, Jan 1957 (1♀; USNM). Mombasa, 9 Dec 1951, Deutche Ost Afrika Exp. (1♀; SMN).

MALAWI. Monkey Bay, Lake Malawi, 15 Aug 1943, R. C. Wood (1♀; BMNH).

NAMIBIA. Gross Barmen Resort (22°07′S, 16°42′E; roadside grass and dry river bed at camp), 29 Mar 1984, J. G. H. Londt, B. Stuckenberg (1♂; NMSA).

NIGERIA. Ile-Ife, 25 Apr 1969, J. T. Medler (1♀; USNM). Lagos (shore), 15 Dec 1987, A. Freidberg (2♂, 2♀; TAU). Lagos, Ikoyi, 14 Jan 1966, J. C. Deeming (1♀; CNC). Lagos, Victoria Island (shore), 15 Dec 1987, A. Freidberg (3♂, 1♀; TAU). Niger State, Mariga River (80 km W Mina), 11 Dec 1987, F. Kaplan (1♀; USNM). Yankori, 8–14 Nov 1987, P. Neuenschwander (1♀; TAU). Zaria, Samaru, May–Sep 1979, J. C. Demming (2♂, 4♀; NMWL).

SENEGAL. Dakar, 4–5 Oct 1978, J. Fortin, G. Hevel (1♂; USNM). Brin (3 km SSE), Iguinchor (11 km SW), 9 Nov 1977, L. Cederholm, R. Danielsson, O. Hammerstedt, K-J. Hedqvist, G. Samuelson (1♀; ZIL).

SEYCHELLES. *La Digue:* La Passe (4°20.8′S, 55°49.8′E), 14 May 1997, V. Hollmann (2♀; ZMHB); La Réunion (4°21.8′S, 55°49.6′E), 14 May 1997, V. Hollmann, W. N. Mathis (5♂, 10♀; USNM, ZMHB). *Mahé:* Airport, 7–8 Apr 1986, W. N. Mathis (2♂, 2♀; USNM); Anse aux Pins (4°41.4′S, 55°31.7′E), 2 Apr-3 May 1986, 1997, V. Hollmann, W. N. Mathis (1♂, 1♀; USNM, ZMHB); Anse Soleil (4°44.8′S, 55°27.9′E), 19 May 1997, W. N. Mathis (1♂, 1♀; USNM); Beau Vallon, 24 Mar 1965, W.T. Tams, I.B. Nye (1♂; BMNH); Police Bay (4°48.0′S, 55°31.3′E), 16 May 1997, V. Hollmann, W. N. Mathis (8♂, 5♀; USNM, ZMHB). *Praslin:* Anse Lazio (4°17.6′S, 55°42.1′E), 8–13 May 1997, W. N. Mathis (12♂, 6♀; USNM); Anse Kerlan (4°18.3′S, 55°41.1′E), 9 May 1997, W. N. Mathis (1♀; USNM); Anse Kerlan Farm (4°18.5′S, 55°41.2′E), 13 May 1997, V. Hollmann (1♀; ZMHB); Anse Lazio (4°17.6′S, 55°42.1′E), 8–13 May 1997, V. Hollmann, W. N. Mathis (20♂, 9♀; USNM); Baie Ste. Anne, Anse Takamaka (4°19.6′S, 55°46.3′E), 10–13 May 1997, V. Hollmann (2♂; ZMHB); Fond de L'Anse (4°20.1′S, 55°43.5′E), 11 May 1997, W. N. Mathis (1♂; USNM).

SIERRA LEONE. Freetown (6 km SW; 9°26′N, 13°16′W; in garden), 21 Nov 1993, L. Cederholm, R. Danielsson (1♂; ZIL).

SOKOTRA ISLAND. Hadibu Plains, 14 Dec 1898, W. R. O. Grant (1♂; BMNH).

SOUTH AFRICA. *Eastern Cape:* Algoa Bay, 22 Mar 1896, Brauns (1♂ holotype of *A. hendeli*; NMW); East London (3227Dd; 5 m; coastal dunes), 16 Mar 1972, M. E. and B. J. Irwin (1♀; NMSA); The Haven (3228Bb; coastal dunes), 24–28 Jun 1979, R. Miller, P. Stabbins (1♂; NMSA). *KwaZulu-Natal:* Dukuduku Forest (4 mi W St. Lucia; 2832Ad; 3 m), 26 Nov 1971, M. E. and B. J. Irwin (2♀; NMSA); Dukuduku Forest (E Mtubatuba; 2832Ad), 21 Jul 1973, M. E. Irwin (1♀; NMSA); Dukuduku (between St Lucia and Matubatuba), 7–8 Apr 1960, B. and P. Stuckenberg (2♀; NMSA, USNM); Durban, 27 Feb 1927, L. Bevis (1♀; BMNH); Gillitts (Pinetown District), 28 Dec 1961, B. and P. Stuckenberg (1♀; NMSA); Jamisons Drift (Tugela River), 12 Apr 1974, M. E. Irwin (1♂; NMSA); Kosi Bay Estuary (2632Dd; indigenous bush area), 16–19 Mar 1982, D. A. Barraclough (5♂, 1♀; NMSA); Lebombo Hills, H. A. Junod (1♂, 1♀, 1EX; BMNH); Mtubatuba, 24–25 Mar 1968, P. J. Spangler

(2♂, 1♀; USNM); Ndumu Reserve (Ingwavuma District), Tongaland, 1–10 Dec 1963, B. and P. Stuckenberg (1♀; NMSA); Near Lilani (Ahrens District), Apr 1962, B. and P. Stuckenberg (1♂; NMSA); Oribi Gorge Reserve, Umzinkulwana Valley, 21–28 Nov 1960, B. and P. Stuckenberg (1♂; USNM); Port St. Johns, 20–25 Nov 1961, B. and P. Stuckenberg (1♂; USNM); Salt Rock (28°29′S, 31°15′E; 10 m; caravan park), 5–12 Oct 1991, J. G. H. Londt (1ex; NMSA); Scottsburgh, 15 Nov 1963, B. and P. Stuckenberg (1♂, 3♀; NMSA); St. Lucia Park, 7–8 Oct 1983, A. Feidberg (1♀; USNM); Tugela Ferry (20 km W; 2830Ga; Malaise trap), 26–27 Feb 1977, R. Miller (1♀; NMSA); Umkomaas (NE; 3030Bb; along sand dunes), 21 Jun 1980, R. Miller, R. Stabbins (1♂; NMSA); Umkomaas, South Coast, 11 Oct 1983, A. Freidberg (4♂, 8♀; USNM); Umlalazi Nature Reserve (2831Dd, dune forest and edges), 2–10 Oct 1982, J. G. H. Londt (1♀; NMSA); Umlalazi Nature Reserve (28°57′S, 31°40′E; 20 m; dune forest), 28–29 Jan 1988, J. G. H. Londt (5♂, 7♀; NMSA); Umlalazi Nature Reserve (1.5 km E Mtunzini; 1831Dd; coastal dune vegetation), 30 Dec 1978, R. Miller (1♀; NMSA); Umlalazi Nature Reserve (1.5 km E Mtunzini; 1831Dd; coastal indigenous vegetation), 27 Jan 1979, R. Miller (1♂; NMSA); Umlalazi Nature Reserve (1.5 km E Mtunzini; 1831Dd; coastal indigenous vegetation), 24–25 Mar 1979, R. Miller (1♂; NMSA); Widenham Umbilo, 16 Dec 1914, L. Bevis (1♂, 1♀; BMNH). *Mpumalanga:* Ofcolaco, Selati River (2430Ab), 7–8 Dec 1976, R. Miller (1♀; NMSA). *Northern Province:* Entabeni For. Station, Zoutpansberg Range (2230Cc; grassland), Jan 1975, B. Stuckenberg (1♀; NMSA).

SUDAN. Um Baghot (among hantot ?), 22 Aug 1931, R. C. M. Darling (1♀; BMNH).

TANZANIA. Tarangire National Park (36°10′E, 03°50′S), Dec 1994, D. Grimaldi (1♂; AMNH).

UGANDA. Kilembe, Ruwenzori Range (4500 ft), Dec 1934–Jan 1935 (1ex; BMNH).

ZIMBABWE. Gwaai, 14 Oct 1926, R. H. R. Stevenson (1♀; NMSA). Harare, 9 Jun 1938, A. Cuthbertson (1♀; BMNH).

Country unknown. Torina (Deutsch Ost Afrika Expedition), 4–18 Mar 1952 (1♀; USNM).

ORIENTAL. INDIA. *Karnataka:* Mudigere, 6 Apr 1980, W. N. Mathis, A. Freidberg (1♀: USNM); *Tamil Nadu:* Palni Hills (Kodaikanal; 6500 ft), Mar–Apr 1953, P. S. Nathan (1♂; USNM).

MALAYSIA. Penang (at light trap), 16 Jul 1957, H. T. Pagden (1♀; BMNH).

SRI LANKA. *Central Province: Nuwara Eliva:* Horton Plains, 23 Apr 1980, W. N. Mathis, T. Wijeshine, L. Jayawickrema (2♀; USNM); *Southern Province: Hambantota:* Palatupana Tank, 6 Feb 1975, K. V. Krombein (1♀: USNM).

PALEARCTIC. UNITED ARAB EMIRATES. *Abu Dhabi:* Ruwais, 6 Nov 1985, M. J. Ebejer (1♀; NMWL).

CANARY ISLANDS. *Gran Canaria:* Las Plamas (on garden wall), 12 Nov 1927, Kisluik (3♂, 1♀; USNM); Las Palmas, R. Stora (1ex; BMNH); 1–15 May 1901 (1♂; ZMHB). *Tenerife:* Laguna (6–700 m), 8–30 Jun 1904 (1♀; ZMHB); Puerto de la Cruz (dry sand on shore), 21–26 Apr 1979, C. E. Dyte (2♂, 8♀; BMNH); Puerto Orotava (low herba and brass near beach), 20 Dec–2 Jan 1901 (6♂, 6♀; ZMHB); Jul 1907, Cabrera (1♀; ZMHB).

EGYPT. Heliopolis, 20–22 Oct 1964, E. Hargreaves (ex; BMNH). Egypten (1♀ holotype, 1♂; NMW). *Sinai:* Bir Zrir, 2 Sep 1970, J. Kugler (1♀; USNM); El-Arba'in (Sinai Mountains), 14 Jul 1974, F. Kaplan (1♀; USNM); Danav, 23 May 1981, W. N. Mathis (1♀; USNM); El ’Arīsh, 9 Jan 1917, E. E. Austen (1♀; BMNH); Ein Furtāga, 7 Jul 1969, Kugler (2♂, 3♀; USNM); Ein H̱udra, 9 Jul 1969, A. Freidberg (2♀, 1ex; USNM); Et-Tūr, 25 Jun 1968 (4♂, 1♀; TAU); Feirān, 9 Apr 1973, D. Furth (1♂; TAU); Nuweibá, 14 May 1981, T. Furman (4♀, 5♂; USNM); Ofira (sewage), 21 May

1981, A. Freidberg, W. N. Mathis (11♂, 8♀, 1ex; TAU, USNM); Ofira, 22 Mar 1981, A. Freidberg (1♀; TAU); Ophira Airport, 22 Apr 1980, B. R. Pitkin (1♀; BMNH); Ras Mamlach, 11–15 Apr 1980, B. R. Pitkin (6♂, 4♀; BMNH); St. Katharina, 12 Jul 1969, J. Kugler (1♀; USNM); Taba (1 km S), 10 Apr 1980, B. R. Pitkin (1♀; BMNH); Wadi Feirān, 25 May 1971, A. Freidberg (2♂, 2♀; TAU, USNM); Wadi Hibrān, 11 May 1973, A. Freidberg, F. Kaplan (1♂, 1♀; TAU); Wadi Watīr, 5 Aug 1975, A. Freidberg (1♂; TAU).

ISRAEL. Arava Valley: H̱aẕeva Field School (30°46.8′N, 35°14.6′E; 2 km N; Naẖal Gidron; 110 m), 11 Mar–7 Jun 1995, M.E. Irwin (1♂, 14♀; TAU); H̱aẕeva, Shezaf Nature Reserve (30°46′N, 35°15.4′E; north of water treatment plant, low sandy hummocks in small wadi; 80 m), 24 Mar–20 May 1995, M.E. Irwin (3♂, 4♀; TAU); H̱aẕeva (30°46.3′N, 35°16.3′E; Haẖal Shaẖaq, between agricultural fields; Malaise trap; 110 m), 15 Mar–16 Apr 1995, M.E. Irwin (10♂, 12♀; TAU); 'Iddan (30°48.9′N, 35°16.8′E; naẖal running east of date palm orchard; 110 m; malaise trap), 13 Mar–5 Jun 1995, M.E. Irwin (21♂, 22♀; TAU); 'Iddan Springs (30°49′N, 35°17′E; in damp seep east of spring; 116 m), 13–17 Mar 1995, M.E. Irwin (3♀; TAU); 'Ir Ovot (30°56.8′N, 35°04.4′E; 3 km NW; water tank on hillside), 6 Apr 1995, M.E. Irwin (2♂, 1♀; TAU). Ashqelon, 5 Sep 1960, Fatal (2♂, 5♀; TAU, USNM). Biq'at Bet Ẕayda, 3 May–5 Aug 1973, 1986, A. Freidberg, I. Nussbaum (1♂, 1♀; TAU). 'En Yahav, 20 Sep 1995, A. Freidberg (10♂, 2♀; TAU, USNM). 'Enot Qane ['En Turaba], 30 Apr 1973, D. Furth (1ex; TAU). Herzliyya (beach; Malaise trap), 13 Jan–9 Nov 1975, 1981, 1982, 1994, A. Freidberg, F. Kaplan, D. Simon, I. Susman (31♂, 56♀; TAU, USNM). Mash'abbé Sade, 21 Aug 1986, A. Freidberg (1♂; TAU). Nahal H̱atira, 19 Oct 1983, I. Nussbaum (1♀; TAU). Ne'ot ha-Kikkar, 20 May 1974, A. Freidberg (3♀, 1♂; TAU). Ne'ot Semadar, 21 Jun–29 Aug 1995, A. Freidberg (4♂, 4♀; TAU, USNM). Paran, 19 Sep 1977, A. Freidberg (2♂; TAU). Park HaYarden, 30 Sep 1982, F. Kaplan (1♂; TAU). Qalya, 20 Mar 1980, J. Kugler (1♀; TAU). Qeẕi'ot, 28 Aug 1986, I. Nussbaum (1♀, 1♂; TAU). Ramat-ha-Sharon, 18 Aug 1975, D. Simon (1♂; TAU). Reẖovot, 30 Oct 1931, 1938, J. Aharoni (3♂; TAU, ZMHB). Tel Aviv, 22 Aug–27 Nov 1969, 1971, J. Kugler (13♀; TAU, USNM). Tel Aviv, Abu-Kabir, 13 Sep 1953, L. Fishelsohn (1♂; TAU). Upper Galilee, Park HaYarden, 5 Aug 1986, W. N. Mathis (2♂; USNM). Yotvata, 23 Sep 1962, J. Kugler (1♂, 4♀; TAU). Ẕe'elim, 6 Dec 1976, A. Freidberg (1♀; TAU). Ẕin Wilderness, Naẖal Ẕin at 'En 'Aqrabbim (35°09′N, 39°E; cane-covered, sandy wadi; 61 m; Malaise trap), 27 Mar–15 May 1995, M.E. Irwin (2♂, 2♀; TAU).

OMAN. As-Seefa (coastal sand dunes), 4 Dec 1987, J. J. Ebejer (1♂, 1♀; NMWL). Ghuzayn (date culture), 10 Apr 1985, Paö (1♂; ZIL). Hazm (date palm grove beside Fort on maize, sorghum, and grasses), 19 Oct 1990, M. D. Gallaghler, J. C. Deeming (3♀; NMWL). Mazara (date cult), 6 Apr 1985, Paö (1♂, 5♀; ZIL). Muscat, 10 Apr 1985, P. Ardö (2♂, 2♀; ZIL). Qurm (hotel garden), 5 Apr 1985, Paö (1♂, 5♀; ZIL). Ruwi, Wattayeh, 1–7 Apr 1988, M. D. Gallagher (6♂, 6♀; NMWL). Viti Wadi, 7 Apr 1985, Paö (1♂, 1♀; ZIL). Wadi Bani Kharus (foothill of Jebel Akhdar Lilyah; 810 m; 23°11′N, 57°40′E), 18 Oct 1990, M. D. Gallaghar, J. C. Deeming (1♂; NMWL).

SPAIN. Almeria, Oct 1973, Boness (10♂, 6♀; BMNH).

Distribution (Fig. 14).—Afrotropical: Angola, Botswana, Cameroon, Cape Verde Islands (São Vincente), Democratic Republic of Congo, Eritrea, Ethiopia, Gambia, Ivory Coast, Kenya, Namibia, Nigeria, Rwanda (literature), Senegal, Seychelles (La Digue, Mahé, Praslin), Sierra Leone, Sokotra Island, South Africa (Eastern Cape, KwaZulu-Natal, Mpumalanga, Northern Province), Sudan, Tanzania, Uganda, Zimbabwe. Oriental: India (Karnataka, Tamil Nadu), Malaysia, Sri Lanka. Palearctic: Canary Islands (Gran Canaria, Tenerife), Egypt, Israel, Oman, Spain, United Arab Emirates (Abu Dhabi). This is the most widespread species of the genus, and its occurrence at some sites may represent introductions. We suspect this to be the case for the Seychelles and perhaps elsewhere, such as the Indian Subcontinent and Malaysia.

Natural history.—On islands of the Seychelles, the majority of specimens collected by Mathis were associated with sandy areas with sparse to no vegetation that were surrounded by or in close proximity to grass covered habitats. Occasionally this species was found associated with organic debris and other garbage that had accumulated at the high tide mark on sandy beaches.

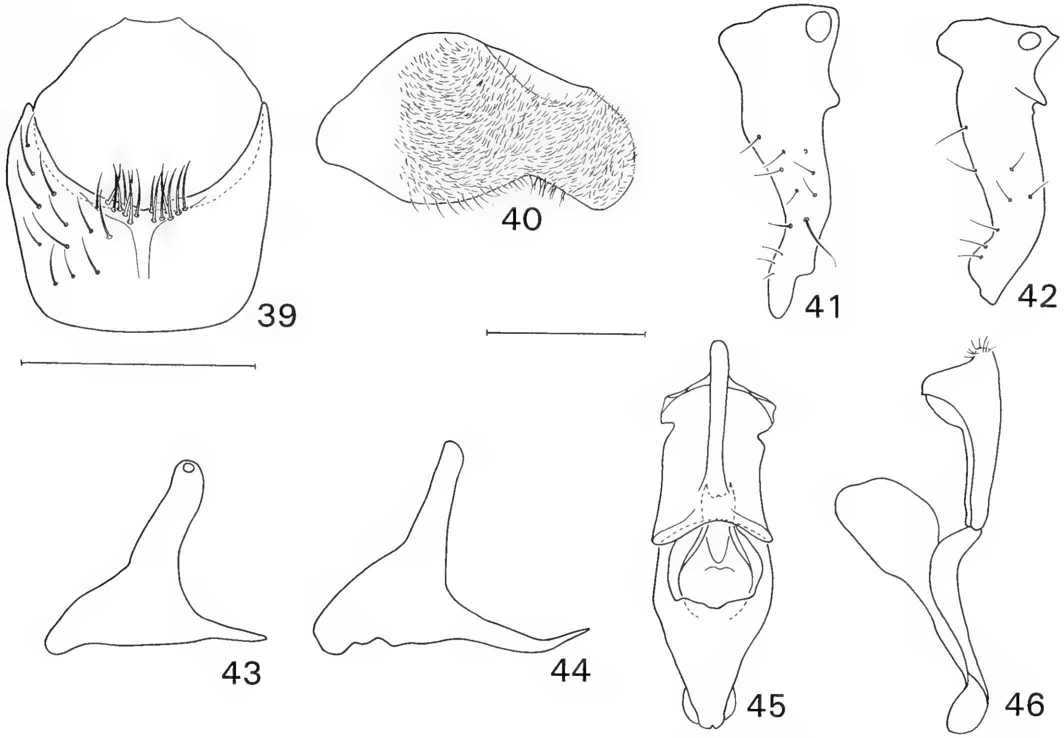
Larvae of this species apparently feed on varied sources of highly organic debris, probably as saprophages. Dr. Amnon Freidberg (personal communication) successfully reared this species on a medium of domestic cat dung in Israel, and Stower et al. (1958) and Greathead (1963) reared adults in Eritrea from damaged egg pods of desert locusts (*Schistocerca gregaria* Forskål).

Observations on mating behavior.—Date: 16 Aug 1986 (Saturday). Time: 10:30 am. Weather: Temperature about 30°C, very slightly breezy, sunny. Location: Beach at Herzliyya, Israel. Shaded area at base of hill, mostly a dune, immediately adjacent to beach (spray belt). Hill covered with *Oenothera* sp. (introduced; Onagraceae) and *Pancratium maritimum* L. (Amaryllidaceae). Observers: A. Freidberg and W. N. Mathis.

Several specimens were observed running over the sandy substrate, primarily in the shade. Their wings were parted at about 80° and occasionally the wings were quickly moved in a scissoring motion. A few females were observed to tap the substrate with their abdomens, perhaps searching for ovipositional sites. When a male came within 5–7 cm of a female, he would immediately pursue her and attempted to mount, apparently without any precopulatory behavior. Mounting was brief, usually 5 seconds or less (range 3–15 seconds based on 4 observations). For one pair we observed the tips of both abdomens touching but could not see if the genitalia of the male engaged those of the female (we assume that they did). After dismounting, the pair would face each other and touch their extended probosces intermittently for 10–20 seconds. While thus touching, the male and/or female would scissor its wings, the opposite sex would remain essentially stationary, with its wings parted at nearly 150°. We could not determine whether trophallaxis occurred with the touching of probosces. While touching probosces there was apparently some foreleg-to-head touching.

Remarks.—Wiedemann described this species twice and in two different genera. As species of *Actocetor* are striking and unlikely to be overlooked, we suspect that Wiedemann failed to examine specimens in his own collection (he may have returned some specimens and did not have ready access to them, did not consult his previously published description, or his memory faltered). Regardless, our study of Wiedemann's primary types clearly revealed that the syntypes of both names are conspecific, with *A. indicus* having priority as the senior synonym. In view of the widespread distribution of this species, particularly in the Afrotropical Region, it is unfortunate that the senior synonym, *A. indicus,* alludes to an area on the periphery of this species' distribution where it may represent an introduction.

The comparison of the male terminalia of the paratype of *A. margaritatus panelii* with those from India and Sri Lanka indicates that both are conspecific and thus the names are synonyms despite the lack of characteristic microtomentum on tergites 3–5. The microtomentum on the abdomen is also variable in other specimens, especially on the 4th tergite. This was particularly evident in specimens from a single site in Nigeria where a majority of the specimens have a wide band of microtomentum and a few,



Figs. 39–46. Structures of the male preabdomen and terminalia of *Actocetor nigrifinis*. 39, Fifth sternite and hypandrium, ventral view (only left side showing setae). 40, Presurstylus, posterior view. 41, Postsurstylus, lateral view (Sri Lanka. Padaviya). 42, Same (Malaysia. Sabah: Kota Kinabalu). 43, Postsurstylar process, posterior view (Sri Lanka. Padaviya). 44, Same (Malaysia. Sabah: Kota Kinabalu). 45, Aedeagus, aedeagal apodeme, dorsal view. 46, Same, lateral view. Scale bar equals 0.3 mm for Fig. 39 and 0.1 mm for Figs. 40–46.

including females, have sparse to no microtomentum. The structures of the male terminalia were compared directly in detail and are the same, and we are thus of the opinion that they are conspecific.

The holotype of *A. hendeli* de Meijere bears only a very narrow band of microtomentum on the 4th tergite and is otherwise metallic, bluish black. Although an entirely bluish black abdomen also occurs elsewhere, specimens often have some yellowish orange to red color on at least the basal 2–3 tergites. The structures of the male terminalia of the holotype are virtually identical to those of typical *A. indicus*, and we consider these specimens to be conspecific. Thus, *A. hendeli* is also a synonym of *A. indicus*.

Actocetor (*Actocetor*) *nigrifinis* (Walker)
(Figs. 39–47, 50)

Opomyza nigrifinis Walker 1860: 168.

Actocetor nigrifinis: Cogan and Wirth 1977: 328 [generic combination].

Actocetor beckeri de Meijere 1916: 264.—Cogan and Wirth 1977: 328 [Oriental catalog].—Mathis and Zatwarnicki 1995: 22 [world catalog].—de Jong 2000: 36 [status of syntypes]. **New synonym.**

Actocetor elegans Hendel 1917: 41.—Cresson 1929: 171 [comparison with *A. margaritatus*].—Cogan and Wirth 1977: 328 [synonymy with *A. beckeri*; Oriental catalog]. **New synonym.**

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small to medium-sized shore flies, body length 2.40–3.70 mm.

Description.—*Head:* Arista with 10–13 dorsal rays. Gena high, higher than height of pedicel, gena-to-eye ratio 0.22–0.30.

Thorax: Mesonotum densely microtomentose, reddish gray to whitish gray, pleura whitish to silvery gray; 2 more or less short, brown bars may be present anteriorly, separated by width equal to that separating prescutellar acrostichal setae; rings at bases of larger setae (prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae) usually not dark brown; scutellum with apical ½–¾ dark brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 50) normally developed with wide anal angle; alula narrow, bandlike, bearing long setulae (length twice height of alula) along posterior margin; vein R_{4+5} bearing 5–6 setae basad of crossvein r-m; wing pattern as follows: cell c with basal ½ white; cell r_1 with 1 sub-basal rectangular spot; cell r_{2+3} with 2 spots, basal spot in line with spot in cell r_1, apical spot, transversely oval/rectangular, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with sub-basal rectangular spot in line with anterior spot in cell r_1, a subcircular, medial spot, in line with crossvein dm-cu, and an apical spot; discal cell with a wide, U-shaped, basal spot (apical arm sometimes constricted or appears to be separated) and a subapical, transversely oval-rectangular spot; cell m with a transversely oval-rectangular spot near middle; cell cua_1 with a large, basal rectangular white and a subapical, transversely trapezoidal spot, vein CuA_1 straight; costal vein ratio 0.65–0.87; M vein ratio 0.94–1.17. Halter stem yellow; knob whitish yellow and distinctly clubbed. Legs generally whitish yellow to yellow; forecoxa and base of femora sometimes with whitish gray to gray microtomentum laterally.

Abdomen: Entirely shiny but with gray microtomentum on base of 1st tergite; color of tergites 1–3 more or less yellowish red, remaining tergites metallic black; 5th sternite of male as in Fig. 39. Male terminalia (Figs. 40–46): epandrium higher than wide, somewhat narrowed dorsally; presurstylus (Fig. 40) large, ventromedial surface with a small emargination, bearing 1 round to oval lobe medially; postsurstylus (Figs. 41–42) much longer than wide, bearing 3–4, apical setulae, apex simple, narrowed, but not bilobed, widest subapically, then tapered to point; postsurstylar process (Fig. 43) distinctly expanded apically, with anterior portion extended to acutely narrowed process, posterior margin narrowly rounded; aedeagus in lateral view (Fig. 46) highest at base, tapered to narrowly rounded apex, in dorsal view (Figs. 45), with apical ⅔ triangular from a wide base to pointed apex; aedeagal apodeme (Fig. 46) in lateral view subtriangular with angle at attachment with base of aedeagus extended and acutely formed; postgonite in ventral view as a sickle shaped process, relatively narrow through length; pregonite short, simple, bearing 2 setulae apically; hypandrium broadly and deeply pouchlike.

Type material.—The lectotype ♀ of *Opomyza nigrifinis* Walker, here designated to preserve stability and make more universal the use of this name, is labeled "SYN-Type [circular label, green submarginal border, SYN handwritten]/Mak [circular label, gray]/nigrifinis [handwritten]/684/Celebes: Makessar [handwritten]/Actocetor nigrifinis Walk. SYNTYPE 1860 Proc. Linn. Soc. Lond. IV p. 168 (Opomyza) det. J.C. Deeming 1964 [handwritten except for "det. J.C. Deeming 196'"]/LECTOTYPE ♀ Opomyza nigrifinis Walker By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is double mounted (minuten in rectangular block of foam), is in good condition (left midleg and wing missing), and is deposited in the BMNH. A paralectotype ♀ is labeled "SYN-Type [circular label, green submarginal border, SYN handwritten]/Celebes [circular label, gray] 58 142 × [on underside of label, means that specimens were purchased in 1858 and collected by Wallace]/nigrifinis [handwritten, label folded]/Notiphilinae 3/8.01. Czerny [brownish label with squares, handwritten]/ Celebes: Makessar [handwritten]/Actocetor nigrifinis Walk. SYNTYPE 1860 Proc. Linn. Soc. Lond. IV p. 168 (Opomyza) det. J.C. Deeming 1964 [handwritten except for "det. J.C. Deeming 196'")." The paralectotype is double mounted (minuten in rectangular block of foam; head, left fore- and midlegs missing), and is deposited in the BMNH.

The lectotype ♀ of *Actocetor beckeri* de Meijere, here designated to preserve stability and make more universal the use of this name, is labeled "Batavia [Djakarta] (Moara Antjol) [= Moaraantjol] XII. 07 [Dec 1907] Jacobson [handwritten]/Actocetor Beckeri det. de Meijere. type [species name and "type" handwritten; black submarginal border]/HOLOTYPE Actocetor beckeri de Meij det. B.H. Cogan 1971 [handwritten except for "det. B.H. Cogan 197"]/Actocetor hendeli de Meij. Det. B.H. Cogan 1971. [handwritten except for "det. B.H. Cogan 197"]/Actocetor Beckeri de Meijere, 1916 ZMAN type DIPT.0437.1 [red]/LECTOTYPE ♀ Actocetor beckeri de Meijere By Dikow & Mathis [all except "LECTOTYPE" and "By" handwritten; black submarginal border]." The lectotype is double mounted (minuten in rectangular block of foam), is in good condition (minuten has verdigris on it), and is deposited in the ZMAN. In the original description, de Meijere mentioned "Sumpf" (swamp) as part of the type locality. There are also five ♀ paralectotypes that bear the same locality data as the lectotype with the addition of "by Bembex nest." Although Cogan wrote that this specimen is a holotype, de Meijere's original description noted "einige Exemplare" (some specimens) and thus a lectotype designation is needed. Cogan also attached a second label on which "Actocetor hendeli de Meij." was written. Cogan apparently confused the name of this species with *A. beckeri* Hendel, which is preoccupied and needed a replacement name, *A. hendeli,* which de Meijere (1924) provided.

The holotype ♀ of *Actocetor elegans* Hendel is labeled "Ceylon, Colombo./6/VI 02. [6 Jun 1902] Dr. Uzel./Actocetor elegans H. det. Hendel [species name and author handwritten]/Coll. Hendel/HOLOTYPE ♀ Actocetor elegans Hendel [red submarginal boarder; name, author, and gender handwritten]." The holotype is double mounted (minuten in a rectangular block of foam), is in very good condition, and is deposited in the NMW.

Other specimens examined.—ORIENTAL. AUSTRALIA. Cocos-Keeling Islands. Direction Island, 4 Jun 1952, T. G. Campbell (1♀; BMNH).

MALAYSIA: *Sabah:* Kota Kinabalu (17 km S), 19 Aug 1983, G. F. Hevel, W. E. Steiner (1♂, 5♀; USNM); Tanjung Aru Beach, 29 Aug 1983, G. F. Hevel, W. E. Steiner (1♀; USNM); Tomani, 1 Sep 1983, G. F. Hevel, W. E. Steiner (5♂; USNM).

PHILIPPINES. Palawan Brookes Point, Uring Uring, 25 Aug 1961, Noona Dan Expedition (1♀; UZMC). Batangas: Bo. Cale (14°07′N, 121°06′E; 7 km NW Tanauan; ex. *Zea mays* L.), 16 Jul 1977, A. T. Barrion (1♂; CNC).

SRI LANKA. *Central Province. Kandy:* Mahiyangana (51 mi NW; Malaise trap at Hasalaka Irrigation Bungalow), 30 Mar–9 Apr 1971, P. and P. Spangler (1♂; USNM); Peradeniya Botanical Gardens, 25 Jan 1977, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (2♂, 8♀; USNM); Peradeniya (Malaise trap at Botanical Gardens), 26–28 Mar 1971, P. and P. Spangler (2♀; USNM). *Northern Province. Jaffna:* Klinochchi (80 ft), 25 Jan 1977, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (1♀; USNM). *North Central Province. Anuradhapura:* Padaviya (180 ft), 2–8 Nov 1970, O. S. Flint, Jr. (1♀; USNM); Padaviya (180 ft; Irrigation Bungalow), 27 Feb–9 Mar 1970, D. R. Davis, W. Rowe (1♀; USNM). *Polonnaruwa:* Pimburettawa (13 mi S Mannampitiya; 1850 ft), 9–12 Oct 1970, O. S. Flint, Jr.

(3♂; USNM). *Province of Sabaragamuwa. Ratnapura:* Panamure (500 ft), 15–21 Oct 1970, O. S. Flint, Jr. (1♂, 1♀; USNM); Uggalkaltota (350 ft; Irrigation Bungalow), 31 Jan–8 Feb 1970, D. R. Davis, W. Rowe (2♀; USNM). *Southern Province. Galle:* Kanneliya, 27 Apr 1980, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (2♂, 1♀; USNM). *Hambantota:* Kirinda, 25 Apr 1980, W. N. Mathis, T. Wijesinhe, L. Jayawickrima (1♂; USNM); Palatupana, 3–6 Feb 1975, K. V. Krombein, P. B. Karunaratne, P. Fernando, E. G. Dabrera (1♀; USNM); Palatupana Tank, 6 Feb 1975, K. V. Krombein (1♀; USNM). *Province of Uva. Badulla:* Digaluma Falls (1550 ft; black light), 17 Aug 1973, G. Ekis (1♂, 1♀; USNM); Girandurakotte Circ. Bungalow (10 mi NNE Mahiyangana; UV trap), 4–7 Sep 1980, K. V. Krombein, P. B. Karunaratne, T. Wijesinhe, L. Jayawickrema, V. Gunawardane (1♂, 2♀; USNM). *Monaragala:* Agunakolapelessa (on or in leaf litter), 8–9 Oct 1980, K. V. Krombein, P. B. Karunaratne, T. Wijesinhe, L. Jayawickrema, V. Gunawardane (1♂, 10♀; USNM); Agunakolapelessa (Malaise trap), 27–28 Mar 1981, K. V. Krombein, T. Wijesinhe, L. Weeratunge (2♂, 9♀; USNM). *North Province.* Kudattanai (6 mi SE Point Pedro), 13 Feb 1962, H. Andersson, P. Brink, L. Cederholm (1♀; ZIL). *Northwest Province.* Kadalmparu (15 mi N Negombo; at shore of lagoon), 31 Jan 1962, H. Andersson, P. Brink, L. Cederholm (1♂, 1♀; ZIL). *Western Province. Colombo:* Colombo, 18 Apr 1980, W. N. Mathis (8♀; USNM); Colombo, Museum Garden, 28–31 Jan 1975, 6 Jul 1976, K. V. Krombein, P. B. Karunaratne, P. Fernando (2♀; USNM); Colombo, 6 Jun 1902, Dr. Uzel (1♀; NMW); Colombo (swept waste ground), 17 Sep 1963 (1♀; BMNH); Katunayaka (near airport), 16 Jan 1977, K. V. Krombein (1♀; USNM); Ratmalana (9 mi S Colombo; dry grass on sandy beach), 7–13 Jan 1963, H. Andersson, P. Brink, L. Cederholm (2♂, 1♀; ZIL).

THAILAND. Chaing Mai, 5 Dec 1985, K. A. Spencer (1♀; NMWL). Hot (20 km W; 200 m), 17 Oct 1993, F. Kaplan, A. Freidberg (1♂; USNM); KhaoLak Beach (100 km N Phuket), 19 Oct 1993, F. Kaplan, A. Freidberg (1♂; USNM).

Distribution (Fig. 47).—Oriental: Cocos-Keeling Islands, Indonesia (Java, Sulawesi), Malaysia, Philippines, Sri Lanka, Thailand.

Natural history.—Like *A. indicus,* this species apparently also occurs around sandy habitats, at least in part. This suggestion is based on the observation that the paralectotypes of *A. beckeri* (see label data noted above) were collected by a nest of *Bembex,* a genus of solitary wasps known to construct nests in sand.

Remarks.—This is a widespread species in the Orient and is likely to occur in more countries than available locality records indicate. The lack of records from most of the countries of Southeast Asia is particularly noteworthy and probably reflects sampling error rather than the species' absence.

Cogan and Wirth (1977) determined previously that *A. elegans* was a junior synonym of *A. beckeri,* and here we have concluded that both names are junior synonyms of *A. nigrifinis,* a species name that was generally overlooked until Cogan and Wirth (1977) correctly assigned this species to *Actocetor* from *Opomyza* (family Opomyzidae).

Subgenus *Poecilostenia* Bezzi

Poecilostenia Bezzi 1908: 195 [as a genus; type species: *Poecilostenia decemguttata* Bezzi 1908, monotypy].—Wirth 1955: 51 [subgeneric status].

Diagnosis.—This subgenus is distinguished from *Actocetor* sensu stricto by the following combination of characters:

Description.—*Thorax:* Mesonotum generally yellow microtomentose. Wing alula completely reduced, bearing few or no setulae along posterior margin; anal angle straight, cell cua_1 narrower than discal cell; vein R_{4+5} bearing 5–6 setulae on dorsum, basad of crossvein r-m and 5–10 setulae apicad of crossvein r-m; vein CuA_1 conspic-

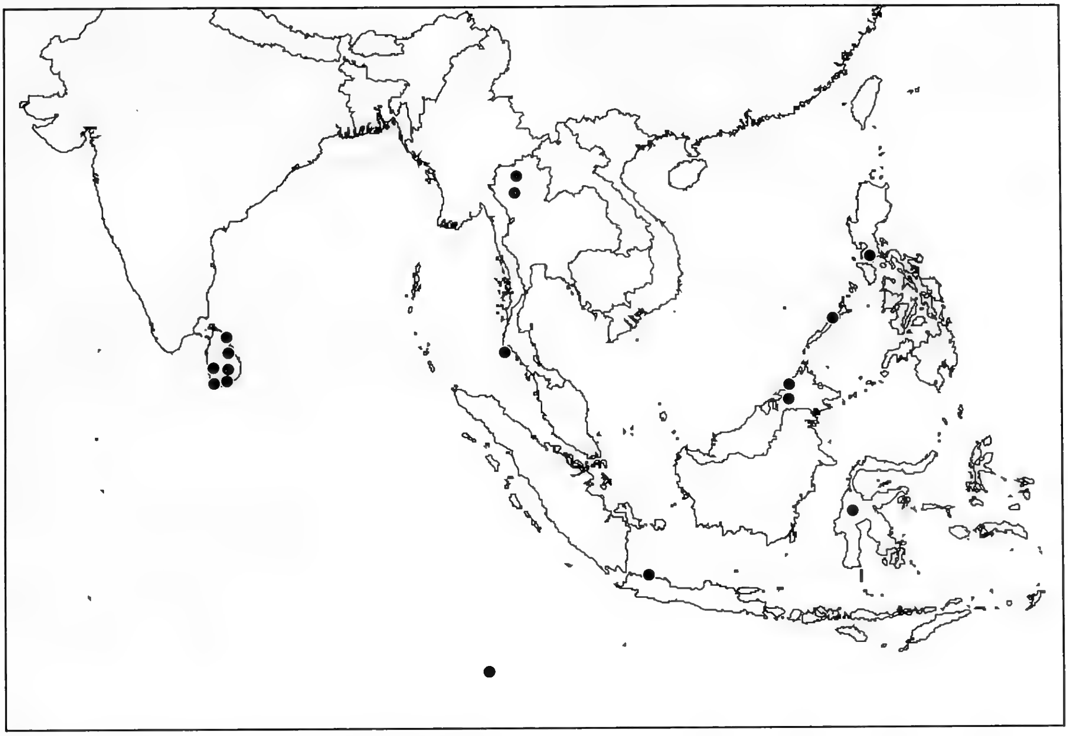


Fig. 47. Distribution map for *Actocetor nigrifinis.*

uously sinuous along posterior margin of discal cell; discal cell with at most 1 white spot. Knob of halter dark brown to black, not distinctly clubbed.

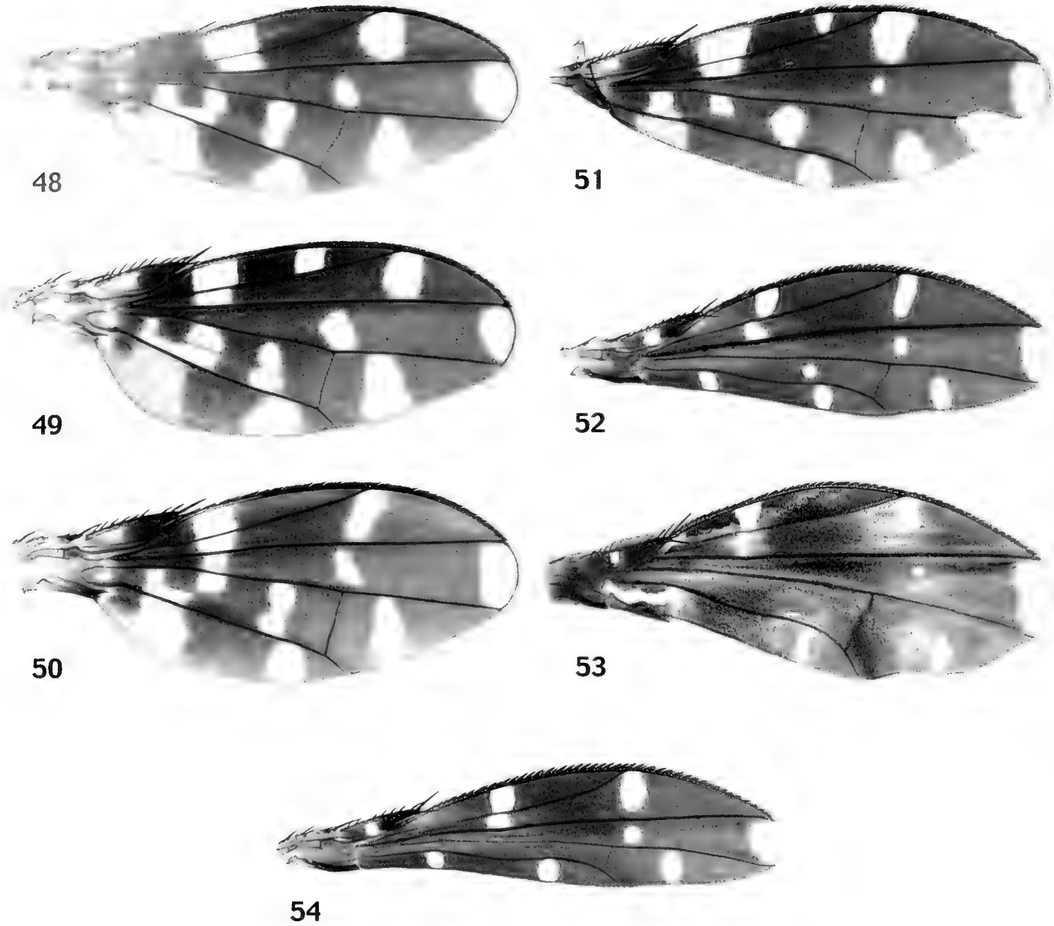
Abdomen: 5th tergite of male bearing 4 well-developed setae along posterior margin; epandrium lacking large setae along dorsum; other structures as in the species descriptions of *A. decemguttatus* and *A. lindneri,* the only species of *Poecilostenia* for which males are known.

Discussion.—Specimens of *Poecilostenia* are uncommon generally and more specifically when compared with *Actocetor* sensu stricto. Although the species can be determined fairly easily, some are represented by a single female. We suspect that additional species will be found in this subgenus as the Afrotropical Region is better sampled.

The subgenus *Poecilostenia* is monophyletic, as substantiated by the following synapomorphies (characters marked with an * are unambiguous): 6*. Color of mesonotal microtomentum yellowish; 11*. Alula completely reduced and bearing few or no setulae along posterior margin; 12*. Cell cua_1 generally narrower than discal cell, and anal margin nearly straight; 13*. Vein R_{4+5} bearing setulae basad and apicad of crossvein r-m; 14*. Anterior margin of vein CuA_1 basad of crossvein dm-cu slightly concave; 20*. Knob of halter dark brown to black; 21*. Knob of halter not distinctly clubbed (only slightly expanded from diameter of stem); 22. Microtomentum on anterior margins of 3rd and 4th tergites with narrow bands (secondarily modified in *A. lindneri*).

Actocetor (*Poecilostenia*) *decemguttatus* (Bezzi)
(Figs. 52, 55–59)

Poecilostenia decemguttata Bezzi 1908: 195 [Botswana. Kang-Khakhea, Kalahari; ST ♂♀, deposition unknown].—Cres-



Figs. 48–54. Wings. 48, *A. hovus.* 49, *A. indicus.* 50, *A. nigrifinis.* 51, *A. afrus.* 52, *A. decemguttatus.* 53, *A. lindneri.* 54, *A. yaromi.*

son 1946: 256 [review, list, South Africa].

Actocetor (*Poecilostenia*) *decemguttatus*: Wirth 1955: 51 [generic combination].—Cogan 1980: 659 [Afrotropical catalog].

Actocetor anormalipennis Séguy 1933: 40.—Cresson 1946: 256 [synonymy with *P. decemguttata* Bezzi].—Wirth 1955: 51 [key].—Canzoneri and Rampini 1995: 254 [list, Sierra Leone].—Mathis and Zatwarnicki 1995: 23 [world catalog]. **New synonym.**

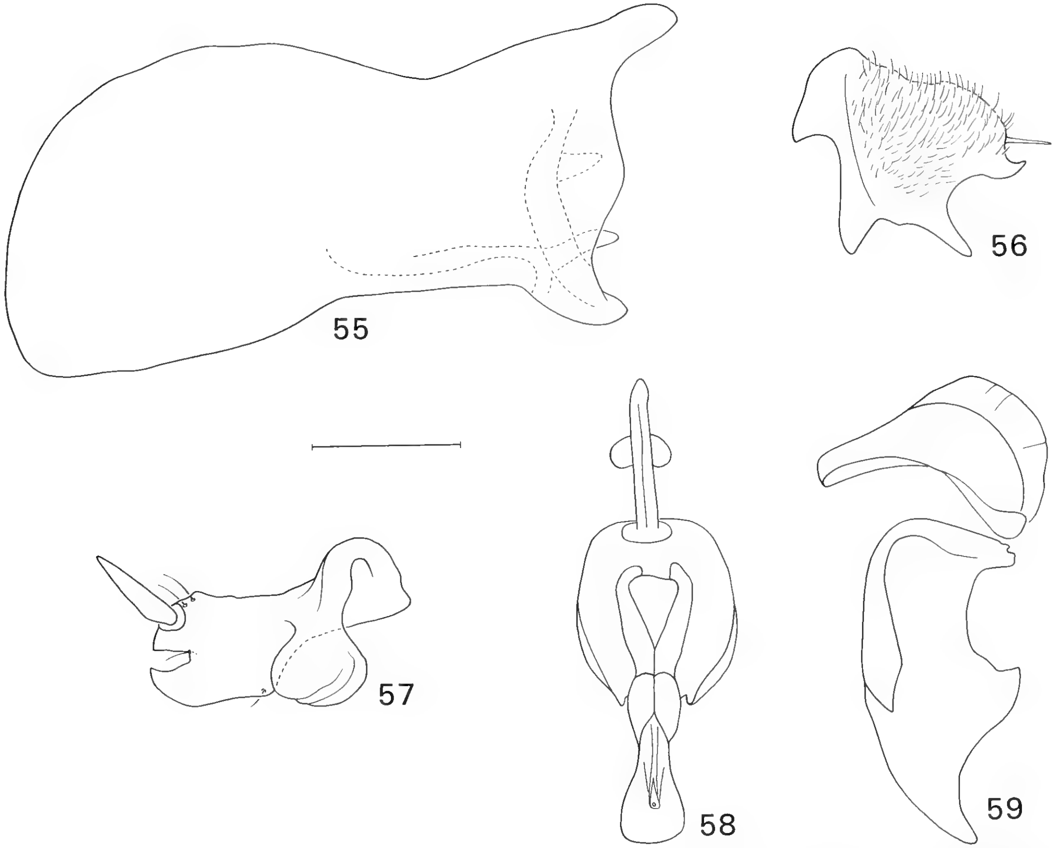
Actocetor abnormalipennis: Cresson 1946: 256 [lapsus, synonymy with *Poecilostenia decemguttata* Bezzi].—Cogan 1980: 659 [Afrotropical catalog].

Actocetor toniatabae Canzoneri 1981: 209 [habitus figure].—Mathis and Zatwarnicki 1995: 22 [world catalog]. **New synonym.**

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small shore flies, body length 2.30–2.90 mm.

Description.—*Head:* Arista with 8–9 dorsal rays. Gena-to-eye ratio 0.20–0.21.

Thorax: Mesonotum densely microtomentose, yellowish brown, pleura concolorous; 2 pale brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; scutellum with



Figs. 55–59. Structures of the male preabdomen and terminalia of *Actocetor decemguttatus*. 55, Hypandrium, lateral view. 56, Presurstylus, posterior view. 57, Postsurstylus, lateral view. 58, Aedeagus, aedeagal apodeme, dorsal view. 59, Same, lateral view. Scale bar equals 0.1 mm.

apical ½ brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 52) very narrow, cell cua_1 narrower than discal cell, anal margin nearly straight; vein R_{4+5} bearing 5 setulae basad and 5 setulae apicad of crossvein r-m; wing pattern as follows: cell c with rectangular white spot basad of subcostal break; cell r_1 with rectangular, medial spot; cell r_{2+3} with 2 spots, basal rectangular/trapezoidal spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a circular medial spot in line with apical spot in cell r_{2+3}, and an apical spot; discal cell with a circular, subapical spot; cell m with transversely oval-rectangular spot; cell cua_1 with 2 spots, rectangular sub-basal spot, and transversely trapezoidal spot in line with spot in discal cell, vein CuA_1 slightly concave between these spots; costal vein ratio 0.70–0.71; M vein ratio 1.17–1.18. Halter stem at base yellowish white, apical part of stem and knob dark brown to black; knob only slightly to moderately expanded from diameter of stem, not distinctly spatulate. Legs generally whitish yellow to yellow.

Abdomen: Mostly shiny, base of 1st tergite with gray microtomentum; base of 3rd and 4th tergites with tiny bands of gray microtomentum; generally metallic black but sometimes with reddish anterior and/or posterior margins of tergites; 3rd and 4th sternites of male rectangular, moderately narrow, 2–3× longer than wide; 5th sternite of male trapezoidal, bearing numerous, mostly evenly scattered setulae, posterior margin evenly concave, lacking a less sclerotized area medially. Male terminalia (Figs. 56–59): epandrium wider than high, bearing numerous setulae, none, especially along dorsum, enlarged; presurstylus (Fig. 56) large, similar to moose antlers, expanded ventral margin bearing 4 prongs, medial prong short, wide, apex curved dorsally as a small point; submedial prong narrow, digitiform, tapered to point; 2 lateral prongs wide basally, tapered to rounded point; postsurstylus (Fig. 57) very robust throughout length, bilobed apically, both lobes well developed, subequal, anterior lobe bearing a well-developed, stout, spinelike seta that extends into hypandrium; postsurstylar process (Fig. 57) short, robust, apex spatulate, round; aedeagus in lateral view (Fig. 59) shoelike, apex pointed, in dorsal view with base wider and lateral extension; aedeagal apodeme in lateral view (Fig. 59) broadly sickle shaped with a moderately prominent, raised keel; postgonite a curved sclerite between juncture of hypandrium and aedeagal apodeme and postsurstylus; postsurstylar process with short stalk, apex somewhat spatulate; pregonite not distinct, perhaps greatly reduced or fused indistinguishably with other structures; hypandrium (Fig. 55) greatly modified, narrow but extended anteriorly like a large, narrow, keel, pouch narrow but deep, bearing pronglike processes that are opposable to spinelike seta of postsurstylus.

Type material.—The syntypes, apparently 1 ♂ and 1 ♀, of *Poecilostenia decemguttata* Bezzi were not located despite searches in Italy (Museo Civico di Storia Naturale, Milano; Dr. Carlo Pesarini) and Germany (Zoologisches Museum, Humboldt Universität, Berlin; Dr. Hella Wendt), and our determination of this species is based on the original description, especially the illustration of the wing. Bezzi (1908) published the following locality data about the syntypes and type locality: "Ein gut erhaltenes Pärchen aus der Kalahari: Kang-Khakhea, Dezember 1904, No. 968."

The holotype ♀ of *Actocetor anormalipennis* Séguy is labeled "MUSÉUM PARIS MOZAMBIQUE ENV. VILA PERV. [Séguy wrote "Vila-Pery" in the original publication; last line of label scratched out; blue]/P. LESNE 1929 [blue]/ouzinai 2 setebre [Séguy wrote "2.X" in the original publication as the day and month]/TYPE [red ink]/Actocetor anormalipennis TYPE E. SÉGUY det 1933 [handwritten except for "E. SÉGUY det 19"]." The holotype is double mounted, is in good condition, and is deposited in the MNHN. The information on this holotype was kindly provided by Dr. Tadeusz Zatwarnicki.

The holotype ♀ of *Actocetor toniatabiae* Canzoneri is labeled "GAMBIA. Toniataba[,] margini mangrovia veget[azione]. alof[ila]. 30.vii [30 Jul] Giordani Soika leg. 1973 [white label glued to a green backing; handwritten except for "Giordani Soika leg. 1973"]/HOLOTYPUS ♀ Actocetor toniatabae m. det. Canzoneri S[ilvano] [red; gender symbol, species name, and "m." handwritten]/Actocetor decemguttatus (Bezzi) det. WNMathis 2000 [species name and year handwritten]." The holotype is double mounted (minuten in a rectangular card), is in excellent condition, and is deposited in the CANZ collection that is now in the MRSN.

Other specimens examined.—AFROTROPICAL. BOTSWANA. Kuke Pan, 21–30 Mar 1930, V.-L. Kal. Exp. (1♀; NMSA). Serowe (Malaise trap), 16–30 Apr 1985, P. Forchhammer (1♀; BMNH). Tlokweng, 15 Mar 1990, J. M. Mashonja, (6♂, 8♀; NMWL, USNM).

GAMBIA. *Western:* Bakau, 15 Nov 1993, J. C. Deeming (1♀; NMWL).

KENYA. Matembur (01°22′N, 35°02′E; 1550 m; Malaise trap), 26–27 May 1980, Lamoral (1♀; NMSA). Nairobi (50 km SE; Rt. A109), 30 Apr 1991, A. Freidberg, F. Kaplan (1♀; USNM). Rift Valley: Nguru-

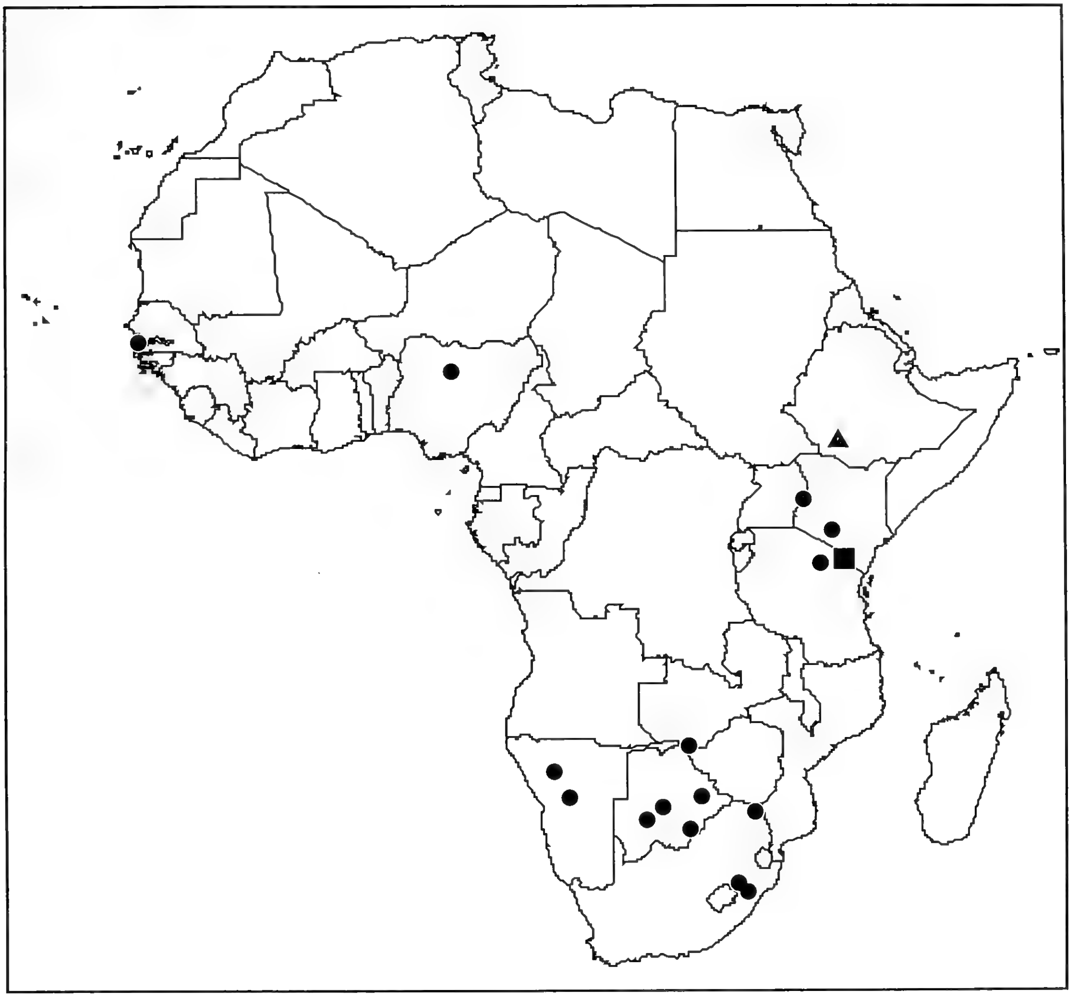


Fig. 60. Distribution map for *Actocetor decemguttatus* (filled circles), *A. lindneri* (filled square), and *A. yaromi* (filled triangle).

man, Oloibortoto River (1°48′S, 36°04′E; Malaise trap), 17–20 May 1999, R. Copeland (1♀; USNM).

NAMIBIA. Outjo (52 km W road 65; 20°14′S, 15°40′E; *Mopane* woodland on a rocky hillside), 24 Mar 1984, B. Stuckenberg, J. G. H. Londt (1♂; NMSA). Okahandja, 2–4 Feb 1972 (1♀; BMNH);

NIGERIA. Zaria, Samaru, Jun 1979, J. C. Demming (3♂, 6♀; NMWL, USNM).

SOUTH AFRICA. *KwaZulu-Natal:* Mhlopeni Nature Reserve (15 km S Muden; 2930Ab), 22 Dec 1983, J. G. H. Londt (1♀; NMSA). Weenen, Nov 1929, H. P. Thomasset (1♂, 1♀; BMNH, NMSA). *Mpumalanga:* Shingwedzi, 9 Feb 1988, D. Simon (2♀; USNM).

TANZANIA. Tarangire National Park (36°10′E, 03°50′S), Dec 1994, D. Grimaldi (2♂, 4♀; AMNH).

ZAMBIA. Livingstone, 16–20 Nov 1958, E. Lindner (1♀; SMN).

Distribution (Fig. 60).—*Afrotropical:* Botswana, Gambia, Kenya, Mozambique, Namibia, Nigeria, South Africa, Tanzania, and Zambia.

Remarks.—This is the only species of the subgenus *Poecilostenia* that is somewhat common, and its distribution in the Afrotropical Region is relatively widespread.

This species was described three times with two of the descriptions being based on single females. Although males were unavailable for two of the type series, we are confident of the conspecificity of the three names based on the stable and consistent wing pattern in the type series of all three names. Our assessment of the stability in the wing pattern is based on study of numerous specimens, including males, in addition to the type series.

Actocetor (*Poecilostenia*) *lindneri* Wirth
(Figs. 53, 61–64)

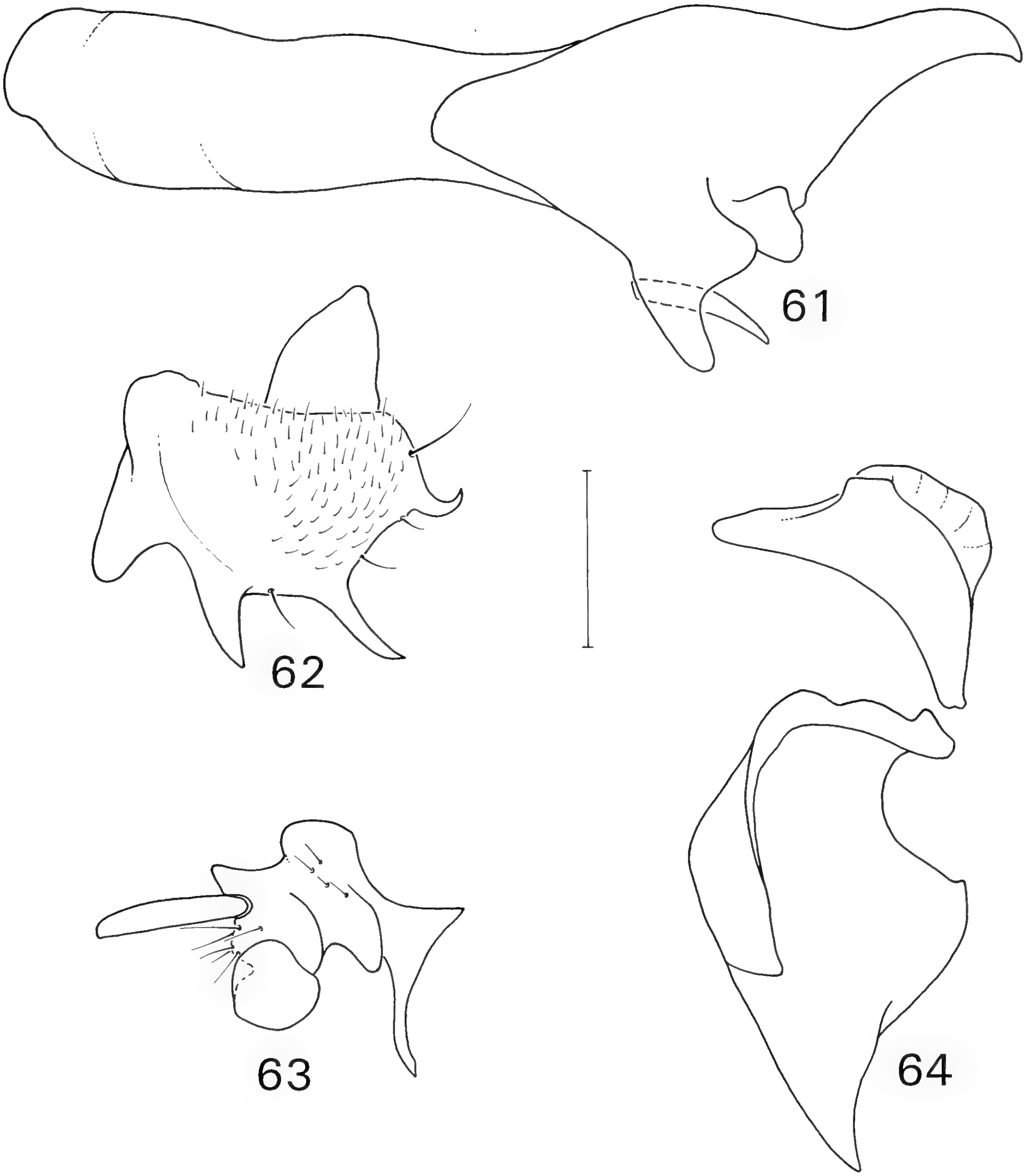
Actocetor (*Poecilostenia*) *lindneri* Wirth 1955: 52.—Cogan 1980: 659 [Afrotropical catalog].—Mathis and Zatwarnicki 1995: 23 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small shore flies, body length 2.90–3.00 mm.

Description.—*Head:* Arista with 10–11 dorsal rays. Gena-to-eye ratio 0.18.

Thorax: Mesonotum densely microtomentose, yellowish brown, pleura concolorous; 2 pale brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; scutellum with apical ½ pale brown, basal portion concolorous with posterior portion of scutum. Wing (Fig. 53) very narrow, cell cua_1 narrower than discal cell, anal margin nearly straight; vein R_{4+5} bearing 7 setulae basad and 7 setulae apicad of crossvein r-m; wing pattern as follows: cell c with rectangular white spot basad of subcostal break; cell r_1 with a circular, sub-basal spot and a rectangular, medial spot; cell r_{2+3} with 2 spots, basal, transversely narrow, rectangular spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a tiny circular, sub-apical spot, and an apical spot; discal cell without spots but with a paler-colored, crescent-shaped bulla on apical half; cell m with narrow, transversely trapezoidal spot; cell cua_1 with 2 spots, 1 sub-basal and 1 subapical narrow rectangular spot, vein CuA_1 concave between these spots; costal vein ratio 0.53–0.72; M vein ratio 1.12–1.15. Halter stem yellowish white basally, apical part of stem and knob dark brown to black; knob only slightly expanded from diameter of stem, not distinctly clubbed. Legs generally whitish yellow to yellow.

Abdomen: Mostly covered by microtomentum: 1st tergite entirely gray microtomentose; 2nd tergite shiny, lacking microtomentum, following tergites entirely microtomentose, basal part gray and apical part brownish; metallic black. Male 3rd and 4th sternites rectangular, moderately narrow, 2–3× longer than wide; 5th sternite of male trapezoidal, bearing numerous, mostly evenly scattered setulae, posterior margin evenly concave, lacking a less sclerotized area medially. Male terminalia (Figs. 61–64): epandrium wider than high, bearing numerous setulae, none, especially along dorsum, enlarged; presurstylus (Fig. 62) large, similar to moose antlers, expanded ventral margin bearing 4 prongs, medial prong short, wide, apex curved dorsally as a small point; submedial prong narrow, digitiform, tapered to point; 2 lateral prongs wide basally, tapered to rounded point; postsurstylus (Fig. 63) very robust throughout length, bilobed apically, both lobes well developed, subequal, anterior lobe bearing a well-developed, stout, spinelike seta that extends into hypandrium; postsurstylar process (Fig. 63) short, robust, apex spatulate, round; aedeagus in lateral view (Fig. 64) shoelike, apex pointed, in dorsal view with base wider and lateral extension; aedeagal apodeme in lateral view (Fig. 64) broadly sickle shaped with a moderately prominent, raised keel; postgonite a curved sclerite between juncture of hypandrium and aedeagal apodeme and postsurstylus; postsurstylar process with short stalk, apex somewhat spatulate; pregonite not distinct, perhaps greatly reduced or fused indistinguishably



Figs. 61–64. Structures of the male preabdomen and terminalia of *Actocetor lindneri*. 61, Hypandrium, lateral view. 62, Presurstylus, posterior view. 63, Postsurstylus, lateral view. 64, Aedeagus, aedeagal apodeme, lateral view. Scale bar equals 0.1 mm.

with other structures; hypandrium (Fig. 61) greatly modified, narrow but extended anteriorly like a large, narrow, keel, pouch narrow but deep, bearing pronglike processes that are opposable to spinelike seta of postsurstylus.

Type material.—The holotype ♀ is labeled "[Tanzania] Jipe-See 20.–23. V. 1952 D. O. Afrika Exp. [blue]/Jipe 21. V 52 [handwritten]/HOLOTYPE ♀ Actocetor linderni W. W. Wirth [red; species name handwritten]/Actocetor (Poecilostenia) lindneri

Wirth det. WWirth [19]54 [species name, author, and "54" handwritten]." The holotype is double mounted (minuten in a cardboard card), is in poor condition (head, left wing, and right fore- and hindlegs are missing), and is deposited in the SMN.

Other specimens examined.—AFROTROPICAL. KENYA. Coast: Muhaka Forest (4°19.47′S, 39°31.45′E; Malaise trap), 2–9 Apr 2000, R. Copeland (1♂; USNM). Eastern: At Athi River (2°38.51′S, 38°21.98′E; Malaise trap), 30 Aug–6 Sep 2000, R. Copeland (1♀; USNM).

Distribution (Fig. 60).—Afrotropical: Kenya, Tanzania.

Remarks.—This species was described from a single female that is in poor condition. We examined an additional female and one male, both from Kenya. Although similar to *A. decemguttatus,* especially structures of the male terminalia, this species is distinguished by characters of the wing. Better sampling of this species may reveal that the wing characters used to distinguish this species are clinal and thus, that this species may be conspecific with *A. decemguttatus.*

Actocetor (*Poecilostenia*) *yaromi* Dikow and Mathis, new species

(Fig. 54)

Diagnosis.—This species is distinguished from congeners by the following combination of characters: moderately small shore flies, body length 2.70 mm.

Description.—*Head:* Arista with 9 dorsal rays. Gena-to-eye ratio 0.15.

Thorax: Mesonotum densely microtomentose, yellowish brown, pleura concolorous; 2 pale brown bars anteriorly, separated by width equal to that separating prescutellar acrostichal setae; scutellum entirely concolorous with yellowish to slightly brownish yellow scutum. Wing (Fig. 54) very narrow, but cell cua_1 wider than discal cell, anal margin nearly straight; vein R_{4+5} bearing 6 setulae basad and 5 setulae apicad of crossvein r-m; wing pattern as follows: cell c with rectangular white spot medially; cell r_1 with rectangular, medial spot; cell r_{2+3} with 2 spots, basal rectangular spot in line with spot in cell r_1, apical, transversely oval/rectangular spot, immediately apicad of merger of vein R_{2+3} with costa; cell r_{4+5} with a circular spot in line with apical spot in cell r_{2+3}, and an apical spot; discal cell without white spot; cell m with transversely oval-rectangular spot; cell cua_1 with 2 spots, a rectangular sub-basal spot, and a transversely trapezoidal spot in line with spot in discal cell; vein CuA_1 concave between these 2 spots; costal vein ratio 0.66; M vein ratio 1.05. Halter stem yellowish white basally, apical part of stem and knob dark brown to black; knob only slightly expanded from diameter of stem, not distinctly clubbed. Legs generally whitish yellow to yellow.

Abdomen: Mostly shiny, base of 1st tergite with gray microtomentum; base of 3rd and 4th tergites with bands of gray microtomentum; generally metallic black but 2nd and 3rd tergites with reddish anterior. Male unavailable.

Type material.—The holotype ♀ is labeled "ETHIOPIA: GAMO GOFA, Arba Minch Springs, 1300m[,] 8.ii.2000 [8 Feb 2000], I. YAROM & A. FREIDBERG/ wing slide [handwritten]/HOLOTYPE ♀ Actocetor yaromi Dikow & W.N. Mathis USNM [red; species' name and gender and "Dikow &" handwritten]." The holotype is double mounted (minuten in a block of plastic), is in good condition (left wing removed and slide mounted), and is deposited in the USNM.

Distribution.—Afrotropical: Ethiopia.

Etymology.—The species epithet, *yaromi,* is a genitive patronym to honor and recognize the contributions of Dr. Ilan Yarom to the study of acalyptrate Diptera. Dr. Yarom collected the holotype.

Remarks.—We are describing this species now despite having only a single female specimen available to us. The species is distinctive, especially the characters of the wing, and confusion with congeners is unlikely.

PHYLOGENETIC CONSIDERATIONS

In the presentation on species-level relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed by a discussion to explain its states and to provide perspective and any qualifying comments about that character. After presentation of the information on character evidence, an hypothesis of the cladistic relationships is presented and briefly discussed. The cladogram (Fig. 65) is the primary mode to convey relationships, and the discussion is to supplement the cladogram and is intended only to complement the latter. In the discussion of character data, an "0" indicates the state of the outgroup; a "1" or "2" indicates the derived states.

Head:

1. Length of 1st flagellomere: (0) relatively long (longer than width of pedicel); (1) short (length subequal to width of pedicel; an autapomorphy for *Actocetor*).
2. Position of antenna on head: (0) positioned near midheight level of head (frons conspicuously longer than wide); (1) positioned high, above dorsal ⅓ in lateral view (an autapomorphy for *Actocetor*).
3. Development of pseudopostocellar setae: (0) setae reduced (as in *Mimapsilopa*); (1) setae well developed, as large as proclinate setae (often or mostly slightly reclinate; a synapomorphy for *Actocetor, Eremomusca, Guttipsilopa,* and *Trypetomima*).
4. Development of facial setae: (0) face bearing 2 well-developed setae; (1) face bearing 4 well-developed setae in a vertical row, dorsalmost 1–2 setae cruciate (a synapomorphy for *Actocetor* and *Guttipsilopa*).
5. Gena-to-eye ratio: (0) variable but gena generally short with ratios of 0.08–0.15; (1) 0.21–0.36 (a synapomorphy for the subgenus *Actocetor*); (2) 0.14–0.20 (a synapomorphy for the subgenus *Poecilostenia*).

Thorax:

6. Color of mesonotal microtomentum: (0) blackish; (1) grayish (a synapomorphy for the subgenus *Actocetor*); (2) yellowish (a synapomorphy for the subgenus *Poecilostenia*).
7. Coloration of scutellum: (0) scutellum entirely concolorous with scutum (as in *A. yaromi*); (1) apicad ¼–½ dark brown (a synapomorphy for *A. afrus* and *A. indicus*); (2) apicad ½–¾ dark brown (a synapomorphy for *A. decemguttatus, A. hovus, A. lindneri,* and *A. nigrifinis*).
8. Color surrounding base of prescutellar acrostichal, posterior dorsocentral, and basal scutellar setae: (0) not distinctly dark brown (as in *A. decemguttatus, A. lindneri, A. nigrifinis,* and *A. yaromi*); (1) distinctly dark brown (a synapomorphy for *A. afrus, hovus,* and *A. indicus*).
9. Development of wing pattern: (0) wing generally hyaline (the plesiomorphic state as in *Mimapsilopa*); (1) wing mostly whitish and conspicuously maculate (an autapomorphy for *Eremomusca*); (2) wing mostly blackish brown with white spots (a synapomorphy for *Actocetor, Guttipsilopa* subgenus *Guttipsilopa,* and *Trypetomima*); (3) wing with anterior margin darkened (a synapomorphy for *Guttipsilopa* subgenus *Nesopsilopa* and some *Discomyza*).
10. Development of apex of vein R_{2+3}: (0) apex normally developed at merger with costa (as in *Actocetor*); (1) vein R_{2+3} with a subapical stump vein (a synapomorphy for *Eremomusca* and *Trypetomima*).
11. Development of alula: (0) alula a well-developed lobe (as in *Guttipsilopa*); (1) reduced to a thin bandlike lobe bearing numerous short or long setulae along posterior margin (a synapomorphy for the subgenus *Actocetor* and the genera *Eremomusca, Mimapsilopa,* and *Trypetomima*); (2) completely reduced and

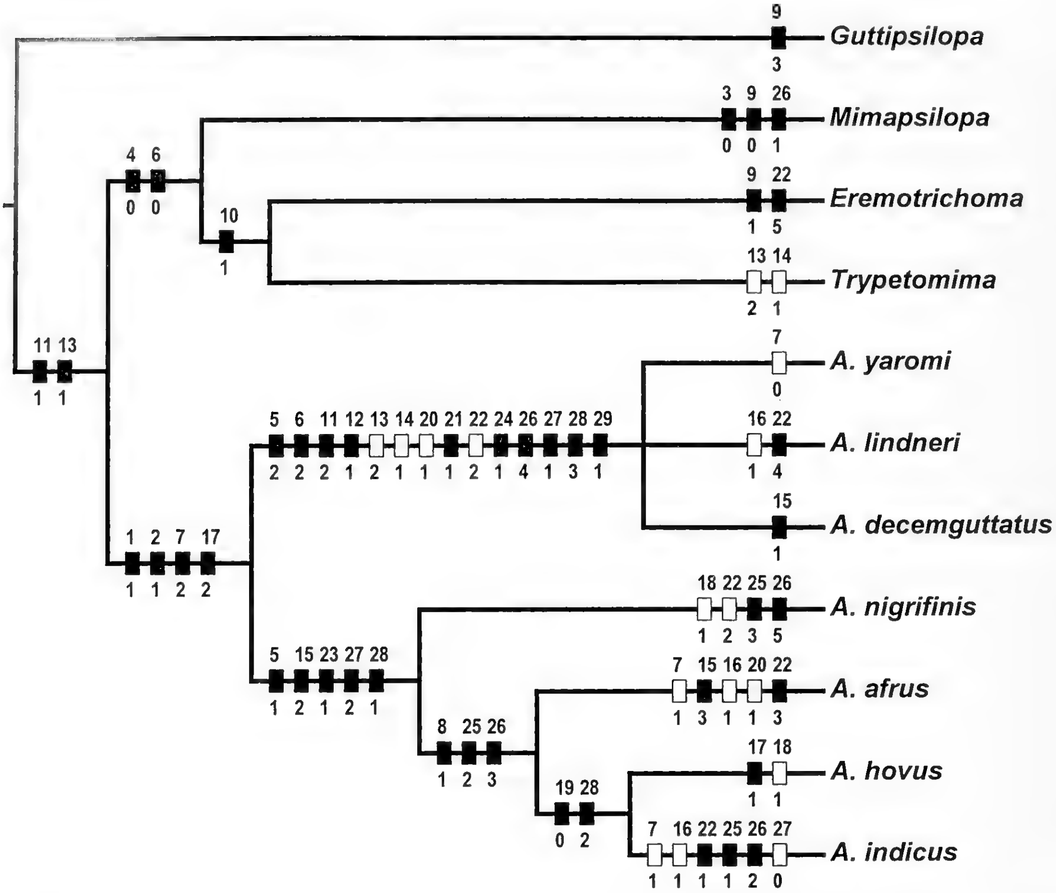


Fig. 65. Cladogram depicting hypothetical cladistic relationships among species of *Actocetor.*

bearing few or no setulae along posterior margin (an autapomorphy for the subgenus *Poecilostenia*).

12. Development of cell cua_1: (0) cell cua_1 broad, broader than discal cell, and anal angle moderately well developed (as in the subgenus *Actocetor*); (1) cell cua_1 generally narrower than discal cell, and anal margin nearly straight (an autapomorphy for the subgenus *Poecilostenia*).
13. Development of setulae on vein R_{4+5}: (0) no setulae present (as in *Guttipsilopa*); (1) setulae only basad of crossvein r-m (a synapomorphy for the subgenus *Actocetor* and the genera *Eremomusca* and *Mimapsilopa*); (2) setulae basad and apicad of crossvein r-m (a synapomorphy for the subgenus *Poecilostenia* and the genus *Trypetomima*).
14. Shape of anterior margin of vein CuA_1 basad of crossvein dm-cu: (0) straight (as in the subgenus *Actocetor*); (1) slightly concave (a synapomorphy for *A. decemguttatus, A. lindneri, A. yaromi,* and *Trypetomima*).
15. Number of white spots in discal cell: (0) no spot (as in *A. yaromi* and *A. lindneri*); (1) 1 spot (a synapomorphy for *A. decemguttatus* and *Trypetomima*); (2) 2 spots (a synapomorphy for *A. hovus, A. indicus,* and *A. nigrifinis*); (3) 3 spots (an autapomorphy for *A. afrus*).
16. Number of white spots in cell r_1: (0) 1 spot (as in *A. decemguttatus, A. hovus,*

A. nigrifinis, and *A. yaromi*); (1) 2 spots (a synapomorphy for *A. afrus, A. indicus,* and *A. lindneri*).

17. Number of setulae on vein R_{4+5} basad of crossvein r-m: (0) no setulae present (as in *Guttipsilopa*); (1) 2–3 setulae (an autapomorphy for *A. hovus*); (2) 4 or more setulae (a synapomorphy for *A. afrus, A. decemguttatus, A. indicus, A. lindneri, A. nigrifinis,* and *A. yaromi*).
18. Costal vein ratio: (0) 0.53–0.73 (as in *A. afrus, A. decemguttatus, A. indicus, A. lindneri,* and *A. yaromi*); (1) 0.73–0.87 (a synapomorphy for *A. hovus* and *A. nigrifinis*).
19. M vein ratio: (0) 0.84–1.00 (as in *A. hovus* and *A. indicus*); (1) 1.01–1.21 (a synapomorphy for *A. afrus, A. decemguttatus, A. lindneri, A. nigrifinis,* and *A. yaromi*).
20. Color of knob of halter: (0) white to yellow (as in the subgenus *Actocetor*); (1) dark brown to black (a synapomorphy for *A. afrus, A. decemguttatus, A. lindneri,* and *A. yaromi*).
21. Shape of knob of halter: (0) distinctly clubbed (as in the subgenus *Actocetor*); (1) knob of halter not distinctly clubbed (only slightly expanded from diameter of stem; an autapomorphy for the subgenus *Poecilostenia*).

Abdomen:

22. Development of microtomentum on abdomen (in addition to microtomentose anterior margin of 1st tergite): (0) entirely bare (as in *A. hovus* and *A. nigrifinis*); (1) anterior margin of 4th tergite with distinct band (an autapomorphy for *A. indicus*); (2) anterior margins of 3rd and 4th tergites with narrow bands (a synapomorphy for *A. decemguttatus* and *A. yaromi*); (3) anterior margins of 3rd, 4th, and 5th tergites with distinct bands (a synapomorphy for *A. afrus*); (4) tergites 3–7 entirely gray and brown microtomentose (an autapomorphy for *A. lindneri*); (5) entirely microtomentose (genus *Eremomusca*).
23. Development of setae on dorsum of epandrium: (0) bearing small setae only (as in *A. decemguttatus* and *A. lindneri*); (1) bearing well-developed, dorsally erect setae (a synapomorphy for *A. afrus, A. hovus, A. indicus,* and *A. nigrifinis;* no male available for *A. yaromi*).
24. Shape of male 3rd and 4th sternites: (0) rectangular, broad, 1–2× longer than wide (as in *A. afrus, A. hovus, A. indicus,* and *A. nigrifinis*); (1) rectangular, moderately narrow, 2–3× longer than wide (a synapomorphy for *A. decemguttatus* and *A. lindneri*; no male available for *A. yaromi*).
25. Shape of male 5th sternite: (0) trapezoidal with slightly concave posterior margin (as in *A. decemguttatus* and *A. lindneri*); (1) trapezoidal with medial weakness or slight indentation on concave posterior margin (an autapomorphy for *A. indicus*); (2) trapezoidal, divided medially into two sclerites (a synapomorphy for *A. afrus* and *A. hovus*); (3) trapezoidal with concave posterior margin with medial weakness and 4–5 setulae on either side of weakness (a synapomorphy for *A. nigrifinis*; no male available for *A. yaromi*).
26. Postsurstylar process: (0) absent; (1) present, cylindrical (an autapomorphy for *Mimapsilopa*); (2) present, clubbed with rounded knob (an autapomorphy for *A. indicus*); (3) present, expanded ventrally and projected to a point posteriorly (a synapomorphy for *A. afrus* and *A. hovus*); (4) present, clubbed but not stalked (a synapomorphy for *A. decemguttatus* and *A. lindneri*); (5) present, distinctly expanded apically, with anterior portion extended to narrow process, posterior margin narrowly rounded (an autapomorphy for *A. nigrifinis*; no male available *A. yaromi*).
27. Postsurstylus: (0) bilobed subapically with a small, digitiform, medial, pointed process (as in *A. indicus*); (1) bilobed apically, both lobes well devel-

Table 1. Matrix of characters and taxa used in the cladistic analysis of *Actocetor* (numbers for characters correspond with those used in the text).

	Characters
	00000 0000111111111122 22222222 12345 6789012345678901 23456789
Taxa	
Guttipsilopa (Nesopsilopa)	00110 1003000000?0??00 00000000
Mimapsilopa	00000 0000010100?0??00 00001000
Eremomusca	00100 0001110100?0??00 50000000
Trypetomima	00100 000211021000??00 00000000
Actocetor (A.) hovus	11111 1212010102011000 01023220
Actocetor (A.) indicus	11111 1112010102120000 11012020
Actocetor (A.) nigrifinis	11111 1202010102021100 21035210
Actocetor (A.) afrus	11111 1112010103120110 31023210
Actocetor (P.) yaromi	11112 2002021210020111 2???????
Actocetor (P.) lindneri	11112 2202021210120111 40104131
Actocetor (P.) decemguttatus	11112 2202021211020111 20104131

oped, subequal (a synapomorphy for *A. decemguttatus* and *A. lindneri*); (2) apex not bilobed, bluntly formed or angulate, tapered to a point toward one side (a synapomorphy for *A. afrus, A. hovus,* and *A. nigrifinis*; no male available for *A. yaromi*).

28. Presurstylus: (0) variable in form, but usually rather simple structures, longer than wide; (1) bearing 1 round to oval lobe medially (a synapomorphy for *A. afrus* and *A. nigrifinis*); (2) bearing 2 lobes along ventral margin, medial lobe much larger, 1 smaller, thumblike process between medial lobe and expanded base (a synapomorphy for *A. hovus* and *A. indicus*); (3) bearing 4 lobes (a synapomorphy for *A. decemguttatus* and *A. lindneri*; no male available for *A. yaromi*).
29. Shape of hypandrium: (0) pouchlike, often moderately deep (as in the subgenus *Actocetor*); (1) very deeply formed, with an extended keel-like process that extends into the abdomen (a synapomorphy for *A. decemguttatus* and *A. lindneri*; no male available for *A. yaromi*).

ANALYSIS, RESULTS, AND CONCLUSIONS

Multistate characters 5, 6, 7, 9, 13, 15, 17, 22, 25, 26, 27, and 28 were treated as nonadditive (−); character 11 is a multistate character that was intuitively kept additive; characters 24 and 29 are autapomorphies that were made inactive (]) for the analysis so that they did not contribute to the calculations of the consistency and retention indices. The autapomorphies were kept in the matrix (Table 1) so that they would appear on the cladogram as evidence corroborating the monophyly of the lineages they support.

Using an exhaustive search, the implicit enumeration (ie*) option of Hennig86, 10 most parsimonious tree (Fig. 65) were generated from the analysis of the 29 characters. These cladograms have a length of 60 steps and consistency and retention indices of 0.83 and 0.83 respectively. The basal nodes in each of the 10 cladograms are identical with variation only in the more derived species within the two subgenera of *Actocetor.*

The matrix was then subjected iteratively to successive weighing (xs w, ie*, cc) to determine a character's contribution or weight (Carpenter 1988, Dietrich and McKamey 1995). The successive weighing stabilized at 418 steps and produced three cladograms that are identical to three of the first 10. A consensus of these three trees resulted in a tree that is identical to one of

Table 2. Analysis of characters based on the cladogram (Fig. 61).

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Steps	1	1	1	1	2	2	4	1	3	1	2	1	3	2	3
Con. Index	100	100	100	100	100	100	50	100	100	100	100	100	66	50	100
Ret. Index	100	100	100	100	100	100	50	100	100	100	100	100	66	66	100
Characters	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
Steps	3	2	2	1	2	1	6	1	1	3	5	3	3	1	
Con. Index	33	100	100	100	50	100	83	100	100	100	100	66	100	100	
Ret. Index	0	100	100	100	66	100	50	100	100	100	100	66	100	100	

the three weighed trees and to one of the original 10 trees. The consensus tree, although with one unresolved lineage (a tritomy), is our cladogram of choice (Fig. 65). The analysis of the characters for the cladogram is given in Table 2 and the weights of the various characters are given in Table 3. Given these character weights, the analysis of the cladogram resulted in revised consistency and retention indices of 0.94 and 0.95 respectively.

Two basal, monophyletic clades are immediately evident within *Actocetor,* and as genus-group names are available for these clades, we are recognizing them as subgenera, *Actocetor* and *Poecilostenia* (otherwise, recognition of these clades as species-groups would have been adequate).

Poecilostenia comprises three species that occur exclusively in the Afrotropics and form an unresolved tritomy. One of these species, *A. yaromi,* is represented by a single female, and as we noted previously, we suspect that additional Afrotropical species will yet be discovered in this subgenus. The most widespread of these three species is *A. decemguttatus.* We predict that the character states found in *A. decemguttatus* and *A. lindneri,* such as the lack of well-developed setae on the dorsum of the epandrium, will also apply to *A. yaromi.*

The subgenus *Actocetor* includes four species, and most of these have widespread distributions. An exception is *A. afrus,* which is thus far only in Senegal and Liberia and which has a partially attenuate wing. The placement of *A. afrus* within *Actocetor* sensu stricto and as the sister species of the lineage giving rise to *A. indicus* and *A. hovus* indicates that an attenuate wing, as found in *A. afrus* and conspicuously so in species of *Poecilostenia,* arose twice. As there are specific and evident differences in the narrowing (see descriptions), we suggest that its independent occurrence in two separate lineages is quite plausible.

A concluding discussion point concerns the geographic origins of *Actocetor.* With *Poecilostenia* being exclusively Afrotropical in distribution, and with most species of the subgenus *Actocetor* also occurring primarily in the Afrotropical Region, we suggest that the genus arose there. We would advocate this more strongly if we had con-

Table 3. Weights (varying between 1–10) and status (additive = +, nonadditive = −, active = [, inactive =]) of characters after successive weighing.

Characters	1	2	3	4	5	6	7	8	9	10
Weight, status	10+[	10+[	10+[	10+[	10−[	10−[	2−[	10+[	10−[	10+[
Characters	11	12	13	14	15	16	17	18	19	20
Weight, status	10+[	10+[	4−[	3+[	10−[	0+[	10−[	0+[	10+[	3+[
Characters	21	22	23	24	25	26	27	28	29	
Weight, status	10+[	4−[	10+[	10+[	10−[	10−[	4−[	10+[	10+[	

clusive evidence on the sister group of *Actocetor*. We suggest that the occurrence of *A. indicus* in the southern Palearctic Region and perhaps in the Oriental Region may represent subsequent dispersion of this species from its Afrotropical origins. An alternative hypothesis is suggested by the cladogram. If *Trypetomima,* which is Oriental and Oceanian in distribution, is the sister group to *Actocetor* and if *A. nigrifinis,* which also occurs in the Orient, is the basalmost species, then the genus could have originated from speciation events in the Orient/Oceanian area with subsequent dispersion to the Afrotropics. It is evident that numerous speciation events occurred in the Afrotropical Region, resulting in the present Afrotropical fauna being comparatively rich.

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BIOLOGY AND IMMATURE STAGES OF *OCHROTRICHIA FOOTEI* (TRICHOPTERA: HYDROPTILIDAE), A NEW MICROCADDISFLY FROM A TORRENTIAL MOUNTAIN STREAM

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Abstract.—The egg, larvae, pupa, and adult male of ***Ochrotrichia footei*, n. sp.**, taken from waterfalls in southern California are described. The species is univoltine, with early instars present during the summer months, and overwintering as fifth instars within their cases. First instars hatch from eggs deposited in abandoned pupal cases attached to vertical rock faces. Gut contents analysis and laboratory observations of living larvae indicate that larvae are scrapers of periphyton, including diatoms, green algae, cyanophytes, and fungal hyphae. The generalist trophic ecology of *O. footei* may be a preadaptation that allows this species to thrive in a harsh and variable environment.

Key Words: *Ochrotrichia footei,* microcaddisflies, new species, streams, larvae, scrapers, diatoms, Bacillariophyta, Cyanobacteria, Chlorophyta

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The number of described species of microcaddisflies (Trichoptera: Hydroptilidae) from North America has been growing steadily during recent years (e.g., Harris and Sykora 1996, Moulton et al. 1999, Harris and Huryn 2000). *Hydroptila* and *Ochrotrichia* are the two most speciose genera with more than 50 and 100 species, respectively (Morse 1993), and most of the newly described species are placed in these genera. Despite efforts to catalog the species richness of the Hydroptilidae, the small size and often cryptic habits of the immature stages have created a lag in studies of their natural history and life cycles. Indeed, of the 300+ species from North America, larva/adult associations are known for only approximately 10% (Wiggins 1996, Keiper 1998, Keiper and Walton 1999).

Species of *Ochrotrichia* are found in lotic habitats (Wiggins 1996) where they are frequently associated with algal mats (Flint and Herrmann 1976; Keiper and Foote 1998, 1999, 2000; Keiper and Walton 2000) or surfaces of rocky substrate where they scrape periphyton (Vaillant 1984, English and Hamilton 1986). It appears that *Ochrotrichia* larvae are equipped with robustly cusped mandibles that allow them to either scrape relatively smooth substrates, macerate biofilms, or pierce cells within filaments of the green alga *Cladophora* (Vaillant 1984, English and Hamilton 1986, Keiper 1999, Keiper and Foote 2000, Keiper and Walton 2000). The only food sources reported for *Ochrotrichia* immatures are *Cladophora* and periphytic diatoms (Keiper and Foote 2000, Keiper and Walton 2000). Early instars do not build portable cases, whereas the fifth, and final, instar constructs either a bivalved purse-like case, or a dome-shaped case (Ross 1944, Wiggins 1996).

During the summer of 1999, *Ochrotrichia* adults of a new species were reared from larvae collected from a southern California stream. We describe the male, egg, larvae, and pupa, and give details on its natural history and feeding habits.

MATERIALS AND METHODS

We collected larvae from Fullers Mill Creek in the San Bernardino National Forest of western Riverside County, near the city of Idyl Wild. Diatom-encrusted rock and algal mats were brought back to the laboratory with living larvae and placed in petri dishes or aerated rearing chambers (Keiper and Foote 1996). Periphyton was scraped with a knife and scooped into collecting vials to obtain early instars. Larval behavior and development was observed, and adults reared from pupae. All laboratory observations of living material were made at 20°C, and a 12:12 light:dark photoperiod maintained with incandescent lights.

Representative immature stages were fixed in Kahle's solution (Wiggins 1996) for 24 h and then preserved in 70% ethanol. Adults were placed directly in ethanol. Immatures were described following the methods of Keiper and Foote (1999). Because the case size for fifth instars varied between dates of collection, larvae and cases were measured separately for each date.

On 27 September 1999 and 18 May 2000, fifth instars were collected with forceps and placed directly into hot water carried in the field in an insulated thermos. After approximately 30 s, larvae were transferred to vials of 10% formalin for preservation. In the laboratory, formalin-preserved specimens were dissected, and the guts removed and smashed on a microscope slide with glycerin and a cover slip. The gut contents were described and enumerated for 5 larvae from May and 9 larvae from September. Descriptions of adults and larvae followed the terminology of Marshall (1979) and Wiggins (1996), respectively.

The collecting site, Fullers Mill Creek, is a low order, snow-melt stream. Due to the remoteness of the site and rugged terrain, the source was not found. The stream forms cobble-strewn channels and also cascades over bedrock, creating numerous waterfalls and madicoles. During the spring and early summer, the habitat is torrential and difficult to access. As the summer progresses and less snow-melt is available, the water slows to a trickle, and many areas bordering the stream remain wet from capillary action only. The green alga *Spirogyra* and the cyanophyte *Cylindrospermum* were visible in some areas, the red alga *Lemanea* was present at cascades, and rocky surfaces were frequently brownish-green with diatoms, unicellular green algae, and filamentous cyanophytes. Mosses were abundant at peripheral slash zones.

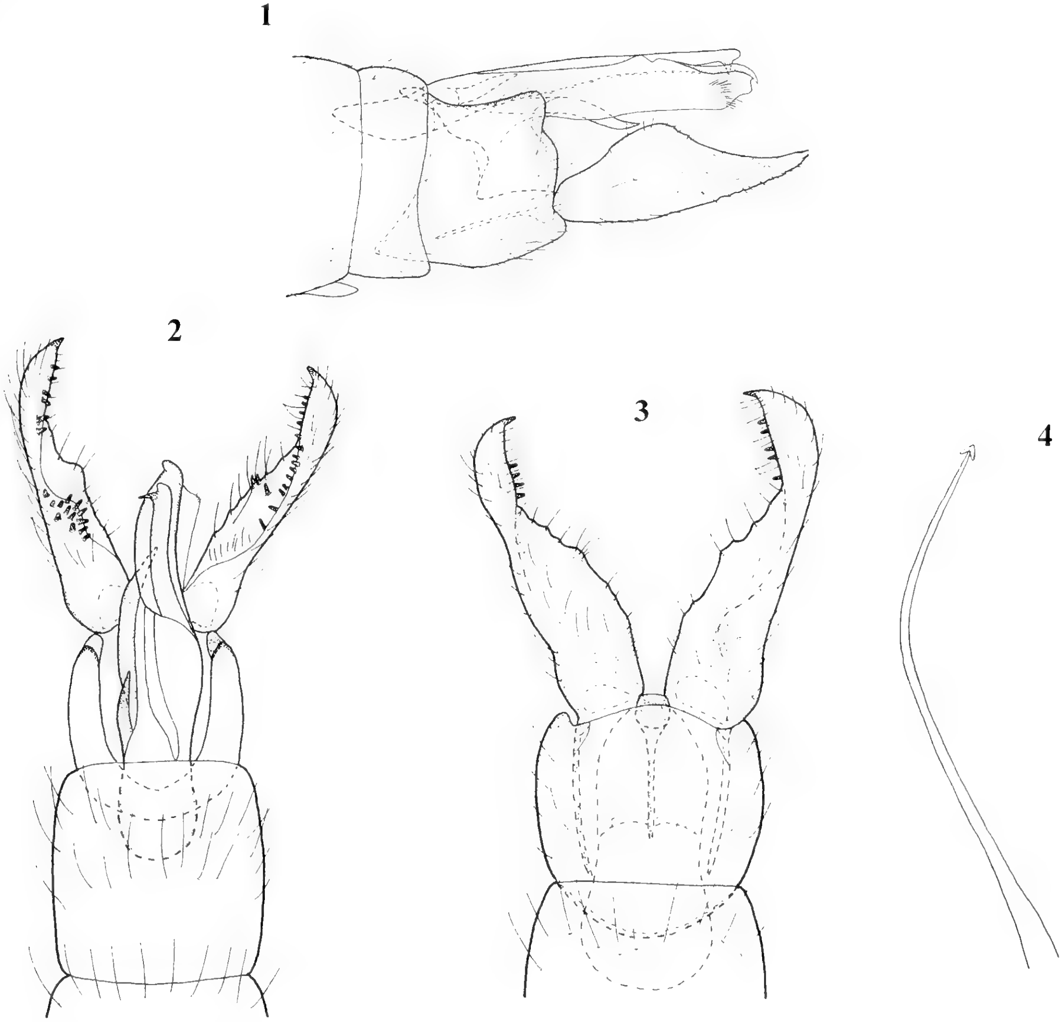
Larvae were collected from three waterfalls at approximately 1,800–1,900 m ASL, each with abundant mosses and diatoms. Each area had a central spill-way where most of the water ran, as well as lateral splash zones. Each area was open to the sunlight, and a variety of trees, mostly oaks (*Quercus* spp.) and pines (*Pinus* spp.), grew along the margins of the stream.

RESULTS

Ochrotrichia footei Keiper and Harris, new species

(Figs. 1–4)

Adult male.—Length 3.5 mm. 31 antennal segments. Brown in alcohol. Abdominal segment VII with short ventromesal process; segment VIII ventrally angular; segment IX square in lateral view, reduced to narrow bridge dorsally (Fig. 1). Segment IX deeply incised mesally in dorsal view (Fig. 2), but rounded ventrally, with shallow lateral incisions posteriorly, a pair of lateral apodemes at outer juncture with inferior appendages (Fig. 3). Tenth tergum bearing several elongate processes, distally with narrow mesal process tipped with heavy spine subapically, anteriorly with pair of acute lateral processes on right margin, anteromost process short, posteromost process



Figs. 1–4. *Ochrotrichia footei,* male terminalia. 1, Lateral. 2, Dorsal. 3, Ventral. 4, Phallus.

elongate and curving inward (Fig. 2); in lateral view segment X thin and elongate, large spine basolaterally and ventrally, dorsal process ending in downward projecting spine, remainder of segment rectangular, with narrow, downward curving posterior sclerite, tuft of fine hairs laterad (Fig. 1); in ventral view with basomesal process, thin anteriorly and rounded posteriorly (Fig. 3). Inferior appendages in lateral view triangular, distally tapering to thin, sclerotized apex (Fig. 1); in dorsal view rectangular, with series of short pegs on inner margin, heavier spine at apex, right inferior appendage with lobe near base bearing numerous short pegs, left inferior appendage with several short pegs on inner margin near midlength (Fig. 2); in ventral view wide basally, tapering to midlength, distally rounded on outer margins, with short pegs on inner margin (Fig. 3). Phallus tubular and thin, small triangle at apex (Fig. 4).

Diagnosis.—*Ochrotrichia footei* appears to be most similar to *O. salaris* Blickle and Denning in the overall configuration of tergum X. Both species have an elongate mesal process which terminates in a lateral spine, and both species have a pair of lateral

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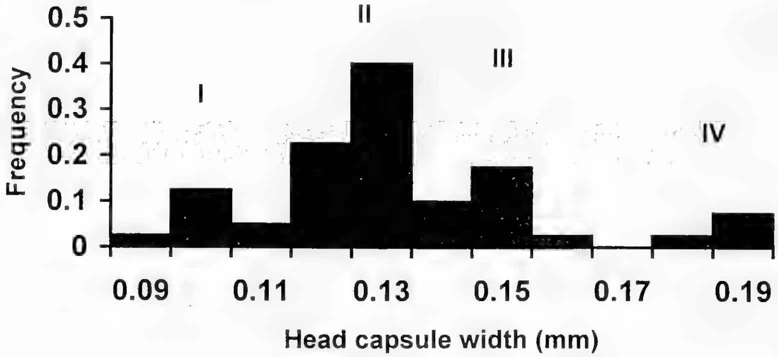


Fig. 5. Histogram of head capsule width for field-collected early instar *Ochrotrichia footei* (n = 40). Numbers placed over peaks indicate estimated instar.

processes. However, the inferior appendages of the new species are triangular in lateral aspect, more similar to those of *O. mono* (Ross) than to those of *O. salaris,* which are narrow at midlength and bear heavy spines from the ventral margin, both anteriorly and posteriorly. The features of the tenth tergum in combination with the shape of the inferior appendages will serve to readily identify *O. footei.*

Type material.—Holotype, ♂: United States, California, Riverside County near Idyl Wild, Fullers Mill Creek, reared from larva collected 29 June 1999, emerged 7 July 1999, J. B. Keiper; deposited at the Cleveland Museum of Natural History, Department of Invertebrate Zoology. Paratypes: 1 ♂, 4 ♀, same location as holotype, except reared from larvae collected 27 June 1999, J. B. Keiper; 2 ♂ pupae, collected 3 July 2000, J. B. Keiper. Paratypes deposited with holotype male, except for 1 male and 2 females (27 June 1999) deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Egg.—Round, chorion colorless, no surface markings evident; embryo bright yellow, developing dark brown to black eye spot with age. Maximum diameter 0.20–0.23 mm ($\bar{x}$ = 0.21 mm). (n = 10).

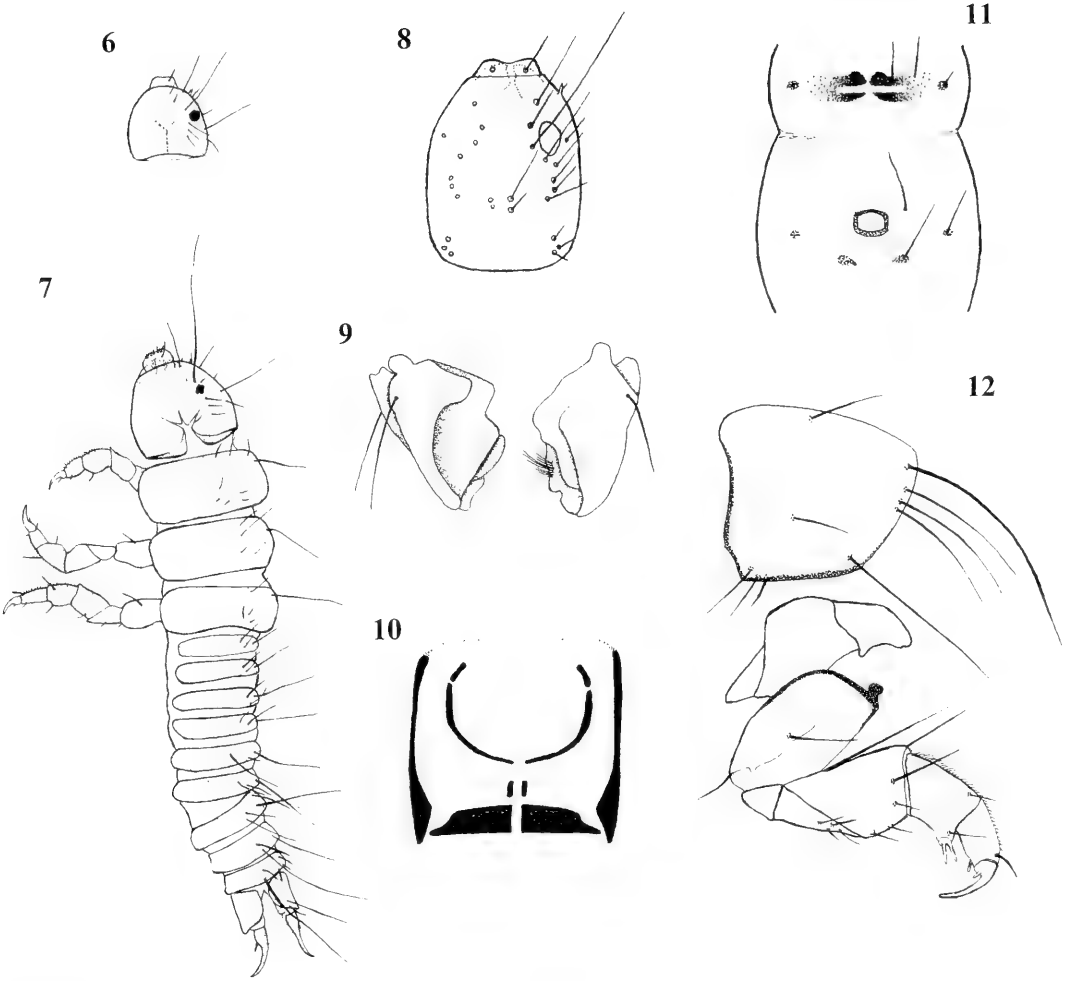
Larvae.—Except for field-collected fifth instars and first instars obtained from eggs in the laboratory, determination of larval stadium was only possible by measuring the head capsule width of field material (n = 40 early instars). Using peaks in a histogram we approximated head capsule width (Fig. 5). Instars 1-4 without cases, as is typical for Hydroptilidae (Wiggins 1996).

First instar: Flattened dorsoventrally, non-sclerotized areas of body white, nearly transparent. Head: width 0.09–0.10 mm, pale brown, posterior margin with thin brown band, sutures evident, newly hatched larvae lacking coloration except for primary setae and eye spot (Fig. 6). Thorax: sclerites pale brown, primary setae well developed. Abdomen: dorsal sclerites rectangular, covering most of dorsum of each segment; segment 10 bifurcate, bearing large anal claws. (n = 10).

Second instar: Similar to first instar, just differing in size and proportions of body parts; sclerites darkening with age. (n = 10).

Third instar: Sclerites darkening considerably. Head: Primary seta near eye spot long, 1.5× length of head capsule, otherwise similar to first instar. Thorax: One pair of long setae laterally on each notal sclerite, others small and weak. Abdomen: Three pairs of strong setae laterally; dorsal sclerite on segment 9 with one pair of long setae positioned mesad, subequal in length to primary seta near eye spot. Otherwise similar to first instar except in size and proportion (Fig. 7). (n = 10).

Fourth instar: Similar to third instar, dif-



Figs. 6–12. *Ochrotrichia footei,* larvae. 6, Head capsule of first instar, right side only with setation. 7, Slide-mounted third instar, dorsal view, right side only with setation, left side only with thoracic legs; note damage to posterior of head capsule and flattening of body a result of slide preparation. 8, Head capsule of fifth instar, right side only with setation. 9, Fifth instar, mandibles, ventral view. 10, Fifth instar, prosternal sclerites, legs removed. 11, Fifth instar, abdominal segments 1 and 2, dorsal view. 12, Fifth instar, pronotal sclerite and fore leg, lateral view.

fering only in size and proportions of body parts, sclerites uniformly dark brown. (n = 4).

Fifth instar: Shape and coloration typical of *Ochrotrichia,* head and thoracic segments mostly dark brown, grading to black or tan in some areas. Head: width 0.15–0.19 mm ($\bar{x}$ = 0.17 mm); eye spot round, black, surrounded by narrow pale ring ca. 0.015 mm wide; position of primary setae as in Fig. 8; longest seta near eye spot approximately same length as head; anterior edge of labrum slightly concave in dorsal view; antenna short, with narrow base, bearing short seta approximately same length as base; right mandible bearing one seta on posterolateral corner, left mandible bearing two (Fig. 9); left mandible with row of hair-like setae on inner margin among dentition; mandibles asymmetrical, each robustly cusped. Thorax: prosternal sclerites dark brown, anterior sclerite small, rectangular, and divided by thin membranous area, two posterior sclerites narrowing laterally, truncate medially (Fig. 10); each sclerite mostly dark brown, with anterior margin lined with dark setae curving anteroventrad; notum with black posterior and lateral margins, black area extending somewhat along anterior margin in darker specimens, never wider than 0.05 mm; legs dark brown to black, foreleg 0.30 mm, midleg 0.36 mm, and hindleg 0.36 mm, leg ratio 0.83:1.00: 1.00; fore tibia and tarsus with anterior margin lined with short hairs, fore tibia with strong ventral projection bearing stout setae, tarsal claw curved with short basal seta (Fig. 12); mesothoracic sclerite with black anterolateral corner; metathoracic sclerite with anterolateral corner produced, tan laterally. Abdomen: milky white, approximately 3.0–3.5× as wide as thorax in lateral view, approximately 2.0× as wide as thorax in dorsal view, somewhat compressed laterally; brown sclerotized rings dorsally on segments 2–8 (Fig. 11), rings on segments 2–4 oblate with lateral edges truncate, rings on segments 5–8 more rounded; segment 1 with dorsal sclerite divided by central membranous band, sclerite fading to pale color laterally; sclerites on abdominal segments 9–10 uniformly dark brown, anal claw somewhat lighter brown than other sclerites, approximately 0.01 mm long; case comprised of minute sand grains in two purse-shaped valves, typical of that for *Ochrotrichia* (Wiggins 1996). (n = 10, mature fifth instars only).

Newly molted fifth instars bear sclerites that are somewhat lighter brown than mature larvae. The dorsomedial sclerite of abdominal segment 1 is less extensive and difficult to see. Otherwise, these young fifth instars are similar except that the abdomen is not swollen and approximately the same girth as the thoracic segments. Length of larvae taken in June were 2.47–4.34 ($\bar{x}$ = 3.31) mm, while those taken in September measured 1.46–3.07 ($\bar{x}$ = 2.12) mm; cases collected in June were 3.21–4.18 ($\bar{x}$ = 3.68) mm in length and contained mature larvae, whereas those cases collected in September contained smaller larvae, and were 1.10–2.04 ($\bar{x}$ = 1.61) mm in length.

Pupa.—Typical of Hydroptilidae; 2 ♂, length 2.7 and 2.9 mm. No distinguishing characters.

Etymology.—Named for Dr. Benjamin A. Foote, Professor Emeritus, Kent State University, who introduced the senior author to Hydroptilidae, in honor of his many contributions to aquatic entomology.

Biology.—One female was observed to emerge on 27 September 1999 from the face of a waterfall. The pharate adult slid down a shallow film of water running over the rock face. After travelling about 20 cm, the adult broke free and flew to mosses adjacent to the water; the exuvia continued to move downward and was lost. The adult sat motionless for approximately one minute, took wing, and was collected with an aerial net. Three other adult females were observed on the same day walking over a water film, each dragging its ovipositor over the water. No oviposition was noted, nor were eggs located during a search of the rock face. Two of the females were collected, brought back to the laboratory alive, and placed in petri dishes with moist diatom-covered rocks. No oviposition occurred.

On 6 July 1999, an empty pupal case was found to contain approximately 50 eggs. The eggs adhered to each other forming a mass within the pupal case. Four more cases with similar egg masses were collected on 27 September. The eggs collected 27 September were placed in a petri dish with stream water and small pieces of diatom-covered rock; the eggs hatched two days later. Although larvae appeared to feed by scraping the substrate, no growth occurred. All larvae died within 5 d. Because only field collected eggs have been studied, the incubation period remains unknown.

In the field, active fifth instars were restricted to areas of noticeable water flow, rather than the wet margins of the waterfalls. Early instars were too small for field

Table 1. Algal and cyanobacterial taxa found in the guts of *Ochrotrichia footei* fifth instars taken in May and September.

Genus	Division	Month Collected	
		May	September
Cocconeis	Bacillariophyta	X	X
Cymbella	Bacillariophyta	X	X
Diatoma	Bacillariophyta	X	
Epithemia	Bacillariophyta	X	
Gomphonema	Bacillariophyta	X	
Surirella	Bacillariophyta		X
Synedra	Bacillariophyta	X	X
Chlamydomonas	Chlorophyta	X	
Oedogonium	Chlorophyta		X
Anabaena	Cyanobacteria		X
Chroococcus	Cyanobacteria	X	
Phromidium	Cyanobacteria	X	
Pseudanabaena	Cyanobacteria	X	
Trachelomonas	Euglenophyta	X	

observations, but scrapings of algal films from areas of flowing water contained early instars while scrapings from wet margins lacked them. Only fifth instars that had attached their cases prior to pupation, or that had temporarily attached their cases to the rock to facilitate case-building efforts, were found in the thin water film at the margins of waterfalls.

Fifth instars brought back to the laboratory scraped diatom covered rocks placed in petri dishes and rearing chambers, but did not form pupae. Three field-collected pupae produced adults (2 ♂, 1 ♀) after ≥10 days. Larvae did not survive long enough in the laboratory for detailed observations of feeding habits.

Gut contents analysis revealed that diatoms were the most common item ingested, and ranged in size from 2.0–20.8 microns in length. Most diatoms were fragmented. Larvae collected in September never had more than 10 diatoms in their guts, whereas those collected in May contained 32–210 diatoms. Eleven algal and cyanophyte taxa were found in the guts of specimens from May, while only six were identified in September samples (Table 1). Fungal hyphae were present in specimens only in May.

Pupae formed aggregations in the field, and were often too numerous to count. All pupal cases were oriented parallel to the direction of water flow. During October 1999 visits to the stream, the rock substrates remained moist only in limited areas and many pupal cases were dry. Collections showed that no cases supported eggs, larvae, or pupae. A number of cases exhibited holes in one lateral valve, possibly made by the predatory behavior of an undetermined species of *Rhyacophila* (Rhyacophilidae) that inhabited the waterfall areas.

DISCUSSION

Fifth instars are separated from all other known *Ochrotrichia* larvae by the combination of uniformly dark brown sclerites, narrow ring around eye spots, left mandible with two posterolateral setae, right mandible with one posterolateral seta, prosternal sclerites separated by a median gap, mediodorsal abdominal sclerites of segment I with longitudinal membranous band, abdominal segments II–VIII bearing mediodorsal ring sclerites with membranous centers, and cases purse-shaped bearing two lateral valves. Immatures are probably restricted to waterfalls or madicolous habitats, which is not uncommon for hydroptilid species (e.g., Ross 1944, Vaillant 1984, Wells 1985, Keiper and Walton 2000).

Much of the life history appears similar to that described for other *Ochrotrichia* spp. (Flint and Herrmann 1976, Vaillant 1984, English and Hamilton 1986, Keiper and Walton 2000). Certain species of Hydroptilidae have been reported to be intimately associated with filamentous algae as piercer/herbivores (Nielsen 1948; Keiper and Foote 1998, 1999, 2000), but *O. footei* never exhibited the algal piercing habit. Waterfalls that range from torrential to virtually dry may preclude populations of Hydroptilidae that exhibit specific trophic habits (e.g., Resh and Houp 1986; Keiper et al. 1998; Keiper and Foote 1998, 2000), thus the relatively generalized feeding habits may have preadapted *O. footei* for existence at Fullers Mill Creek. The mandibles appear well-suited for attacking rock substrates, and allow larvae to consume a variety of materials, similar to that of *O. quadrispina* (Keiper and Walton 2000). There appeared to be a dietary shift from May to September as more diatoms were consumed and a greater number of algal/cyanophyte taxa were present in guts during that period of greatest water flow. During May, three cyanophyte genera were present in guts, whereas *Anabaena* was the only cyanophyte taxon present in September. The green alga *Oedogonium* was the only chlorophyte consumed during late summer, and has been reported as a food source of the hydroptilid *Oxyethira arizona* Ross (Keiper and Walton 1999). The dietary shift was probably not behavioral, but resulted because of a change in the periphyton community as the habitat dried. These observations suggest that categorizing macroinvertebrates into functional feeding groups based on gut contents analysis may lead to spurious results if such analyses are taken from specimens collected from only one time period.

We can infer certain biological details based on laboratory and field observations. *Ochrotrichia footei* is probably univoltine and overwinters as fifth instars. Adults are active during summer months and multiple cohorts of immatures coexist. Small fifth instars with short cases are present in the autumn, and overwinter inside their cases. Larvae seal their cases in preparation for pupation after case building and growth are concluded in the spring. Due to the remoteness of the area, difficulty associated with field observations in torrential streams, and difficulty with rearings, many biological details remain unknown.

A particularly fascinating aspect of the biology of *O. footei* is that females place their eggs in one mass inside of empty pupal cases. Based on laboratory and field observations, it is evident that females leave their cases; parthenogenesis has never been reported in Trichoptera to our knowledge. After mating, females then must find a suitable case for egg deposition. All six cases with eggs were undamaged, and open to the environment through the apical slit in the case formed by escaping pharate adults. Few observations of hydroptilid oviposition have been recorded (but see Nielsen 1948, Resh and Houp 1986, Ito 1997), but some species do create egg masses. The behavioral adaptation of inserting eggs into attached cases may provide certain benefits, such as protection from desiccation, ultraviolet light, predators, or torrential waters.

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INSECTS (DIPTERA, COLEOPTERA, LEPIDOPTERA) REARED FROM WETLAND MONOCOTS (CYPERACEAE, POACEAE, TYPHACEAE) IN SOUTHERN QUEBEC

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Abstract.—Information about feeding habits and host-plants is given for 24 species of insects reared from the stem or leaves of wetland herbaceous monocots, primarily *Carex lacustris* Willd. and *Phalaris arundinacea* L., in southern Quebec. Nineteen species of Diptera in eight families (1 Dolichopodidae, 2 Otitidae, 1 Anthomyzidae, 1 Agromyzidae, 1 Chamaemyiidae, 1 Sphaeroceridae, 11 Chloropidae, 1 Scathophagidae), three Lepidoptera in the families Cosmopterigidae, Elachistidae, and Noctuidae, and two weevils (Coleoptera: Curculionidae) were reared from four species of host plants. Seven species are phytophagous primary invaders, thirteen are secondary invaders (mostly saprophagous) inside the burrows of primary invaders, two are predators of aphids and other invertebrates living on the leaves of the plants, and two have unknown feeding habits.

Key Words: Diptera, Coleoptera, Lepidoptera, ecology, stem-borers, secondary invaders, host plants, wetlands, *Carex, Phalaris*

Emergent wetland plants provide a microhabitat and food source for many insects, especially Diptera (Gaevskaya 1969, Ferrar 1987). The higher Diptera fauna in wetlands is diverse and many species, particularly in the family Chloropidae, are associated with emergent plants such as sedges (Cyperaceae), rushes (Juncaceae) and grasses (Poaceae) (Davis and Gray 1966, Todd and Foote 1987a, 1987b, Pollet 1992). Although there have been several studies on the biology of selected Diptera feeding on wetland monocots (e.g., Valley et al. 1969b, Rogers et al. 1991, Allen and Foote 1992, Wearsch and Foote 1994, Valley and Foote 1996), the host plants and feeding habits are unknown for many species.

Many flies associated with emergent plants are saprophagous secondary invaders of plant tissues damaged by other insects. In many cases, the feeding habits of primary invaders other than Diptera are also poorly known. This study provided the opportunity to obtain biological information on some species of phytophagous Lepidoptera and Coleoptera associated with wetland plants.

This paper documents the results of rearing studies on Diptera and other phytophagous insects associated with emergent wetland monocots in southern Quebec. Host records and ecological information are given for 19 species of Diptera, three species of Lepidoptera, and two species of weevils (Coleoptera: Curculionidae) reared from Cyperaceae, Poaceae and Typhaceae.

MATERIALS AND METHODS

Infested plants were collected from May–October 1999 in sedge meadows of the Lac St. François National Wildlife Area in southern Quebec, and May 2000 at Stoney-

Table 1. Insects reared from *Carex lacustris* and *Phalaris arundinacea* in southern Quebec. COL = Coleoptera; LEP = Lepidoptera; all other species are Diptera.

Trophic Group	*Carex lacustris*	*Phalaris arundinacea*
primary invaders	*Chlorops seminiger*	*Chromatomyia fuscula*
	Cosmopterix fernaldella (LEP)	*Apamea ophiogramma* (LEP)
	Elachista sp. (LEP)	
	Sphenophora costipennis (COL)	
secondary invaders	*Chaetopsis massyla*	*Chaetopsis ?fulvifrons*
	Lasiosina canadensis	*Conioscinella zetterstedti*
	Rhopalopterum atriceps	*Oscinisoma alienum*
	Orthacheta hirtipes	*Elachiptera penita*
		Elachiptera angustifrons
		Eribolus longulus
		Eribolus nana
		Eribolus nearcticus
predators	*Plunomia elegans*	
	Thaumatomyia obtusa	
unknown	*Medetera aberrans*	
	Anthomyza sp.	

croft Pond, adjacent to McGill University's Morgan Arboretum in Ste-Anne-de-Bellevue, Quebec. Infested stems of *Carex, Scirpus* (Cyperaceae) and *Typha latifolia* L. (Typhaceae) were identified by the presence of curled, decumbent, yellowish-brown inner leaves, contrasting with green, straight, healthy outer leaves (Neff and Wallace 1969). Infested stems of *Phalaris arundinacea* L. (Poaceae) were detected by the presence of yellowish terminal leaves and shorter shoots than intact plants. Infested leaves were distinguishable by the presence of mines visible on the leaf surface.

Infested plants were transported to the lab in plastic bags and either examined immediately or refrigerated for later examination. Stems were dissected to locate larvae and any observed feeding behavior was noted. The lower end of each infested leaf was placed in a 1 cm × 5 cm vial filled with water. The vials containing leaves, or small cut sections of stems containing larvae, were placed in a plastic container 4.5 cm in diameter and 7.5 cm deep, covered with fine mesh. These were kept at 22°C in a sealed plastic bag containing moist paper towel in order to keep humidity high. Containers were inspected every 2–3 days for emerged adults. Plants collected late in the season (late August to October) were put in an incubator at 4°C for 1–2 months before dissection to simulate overwintering for the larvae.

Additional collecting in the field using sweep nets and pan traps around host plants provided data on the adult activity of some insect species. All specimens collected and reared are deposited in the Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, except Microlepidoptera, which are in the Canadian National Collection of Insects, Ottawa, ON.

RESULTS

Infested plants were mostly *Carex lacustris,* collected in the Lac St. François National Wildlife Area, and *Phalaris arundinacea,* collected at Stoneycroft Pond. Insects reared from these host plants are listed in Table 1. Species are classified as phytophagous primary invaders, secondary invaders (saprophages and/or facultative predators), and predators of other insects feeding externally on the plant. Ecological observations and previous records of reared species are included in the annotated list below.

Diptera

Medetera aberrans Wheeler (Dolichopodidae).—Two adults were reared from larvae found on the inner leaves of two shoots of *C. lacustris* at a height of 17 and 20 cm from the culm base (Lac St. François, 18.ix.1999, emerged 04.i.2000 (1); same except 01.x.1999, emerged 02.i.2000 (1)). A narrow, brown feeding trail was observed on two leaves of one of the shoots, but no other arthropods were found in association with the *M. aberrans* larvae. The larvae of several *Medetera* species live under tree bark, and are predators of soft-bodied arthropods (Bickel 1985). However, Bickel (1985) noted that *M. aberrans* and related species are more closely related to *Thrypticus* Gerstäcker (a phytophagous genus) and *Dolichophorus* Lichtwardt than they are to *Medetera sensu stricto* and suggested that the larvae of *M. aberrans* may be associated with wetland plants. Although the presence of a feeding trail and the absence of other arthropods might suggest that *M. aberrans* larvae are phytophagous, the evidence is not conclusive and the larval habits remain unknown.

Chaetopsis ?fulvifrons Macquart (Otitidae).—Three adults were reared from two stems of *P. arundinacea* attacked by *Apamea ophiogramma* (Noctuidae) (Stoneycroft Pond, 31.v.2000, emerged 27.vi.2000). Valley et al. (1969a) considered *C. fulvifrons* a secondary invader in the heads of *Echinochloa crusgalli* (L.) (Poaceae) attacked by the phytophagous otitid *Eumetopiella rufipes* (Macquart). Johnson (1921) stated that *C. fulvifrons* injures corn, sugar-cane and onions, but did not indicate whether he considered the larvae phytophagous or saprophagous.

Chaetopsis massyla (Walker) (Otitidae).—Adults were reared from three species of host plants. Most specimens were reared from multiple stems of *Typha latifolia,* usually following primary infestation by a moth or weevil (Lac St. François, 23.vii.1999, emerged 11.viii.1999 (2), 12.viii.1999 (3) and 13.viii.1999 (1); same except 7.viii.1999, emerged 16.viii.1999 (1); same except 12.viii.1999, emerged 17.viii.1999 (1) and 30.viii.1999 (1)); one adult was reared from *C. lacustris* (Lac St. François, 16.vii.1999, emerged 05.viii.1999); three adults emerged from a rotting shoot of *Scirpus fluviatilis* (Torr.) Gray (Cyperaceae) along with an adult of *Pullimosina pullula* (Zetterstedt) (Sphaeroceridae) (Lac St. François, 7.viii.1999, emerged 7.ix.1999). Adults were abundant on *C. lacustris* at Lac St-François. This species was previously reared as a secondary invader from *T. latifolia, C. lacustris* and *Scirpus microcarpus* Presl. (Valley et al. 1969b, Allen and Foote 1992). This is the first record of *C. massyla* from *S. fluviatilis.*

Plunomia elegans Curran (Chamaemyiidae).—Several adults were reared from puparia found between the leaves of *C. lacustris* (Lac St. François, 05.vii.1999, emerged 11.vii.1999 (1); same except 12.vii.1999, found dead 22.xi.1999 (1); same except 23.vii.1999, emerged 02.viii.1999 (1); same except 01.x.1999, emerged 14.ii.2000 (1); same except 27.x.1999, emerged 14.ii.2000 (1)). There are no previous records of the ecology of *Plunomia* spp., but given that all Chamaemyiidae whose feeding habits are known are predators of Aphidoidea and Coccoidea (Ferrar 1987), the larvae probably prey on one of these taxa. Specimens of *Thripsaphis ballii* (Gillette) (Drepanosiphidae) were abundant on *C. lacustris* at the study site and are the likely prey of *P. elegans.* Adults of *P. elegans* were abundant in stands of *C. lacustris* and *C. aquatilis* Wahlenb. by 14 May 1999, peaked in July, and persisted until early September. Unpublished collection data on specimens in the Canadian National Collection of Insects indicate that *P. elegans* lives in wet habitats such as grassy marshes, sedge meadows and bogs.

Chromatomyia fuscula (Zetterstedt) (Agromyzidae).—Four adults were reared from leaf mines in individual leaves of *P. arundinacea* (Stoneycroft Pond, 31.v.2000, emerged 11.vi.2000).This species has been reared from several cereals and wild grasses, including *P. arundinacea,* in Europe (Griffiths 1980); this is the first North American record from this host. Previous Nearctic records were from the grasses *Beckmannia erucaeformis* L. and *Cinna latifolia* (Trev.) Griseb. in western North America (Griffiths 1980).

Anthomyza sp. (Anthomyzidae).—One adult was reared from a larva that was found 10–15 cm from the culm base of *C. lacustris* (Lac St. François, 19.x.1999, emerged 09.ii.2000).The shoot had signs of internal feeding damage but no exit holes or larvae of other species were seen; this suggests that the anthomyzid larva was a primary invader, although this is not certain. The larval feeding habits of the Anthomyzidae are practically unknown (Foote 1991). Some *Anthomyza* spp. have been found between the sheathing leaves of grasses, *Juncus* and *Typha* (Nye 1958, Uffen and Chandler 1978, Ferrar 1987), but it is not known whether the larvae were phytophagous or saprophagous. This specimen was not identified to species because most Nearctic species of *Anthomyza* are undescribed and there is no key to species.

Chlorops seminiger Becker (Chloropidae).—This species was reared as a primary invader from ten *C. lacustris* stems (Lac St. François, 01.x.1999, emerged 28.xii.1999 (1); same except emerged 02.i.2000 (1); same except 19.x.1999, emerged 31.xii.1999 (1); same except emerged 24.i.2000 (1); same except emerged 29.i.2000 (1); same except 27.x.1999, emerged 24.i.2000 (5 from 4 stems); same except emerged 29.i.2000 (1)). Emerging adults were always solitary, except in one case where two flies emerged from the same stem. The mature larvae were deep in the culm, very close to the base. Adults were collected at the study site from mid-May to late June. Sedges from which the adults were reared were collected in October 1999; the larvae are more mature late in the season and damage to *Carex* stems is more evident. The flies probably overwinter as second- or third-instar larvae because larvae collected in October were large (over 0.6 cm long) and because most other chloropid stem-borers of Cyperaceae whose life cycle is known overwinter as second or third instars (Rogers et al. 1991, Wearsch and Foote 1994). This is the first host-plant record for *C. seminiger. Chlorops certimus* Adams and *C. frontosa* Meigen have been reared from *Carex* species (Nye 1958, Rogers et al. 1991) and *Chlorops obscuricornis* Loew is a primary invader of stems of *Eleocharis* (Cyperaceae) (Wearsch and Foote 1994). Most other rearing records of *Chlorops* species are from grasses (Nye 1958, Ferrar 1987).

Conioscinella zetterstedti Andersson (Chloropidae).—Two brachypterous adults emerged from one stem of *P. arundinacea* infested by *Apamea ophiogramma,* along with *Eribolus nearcticus* and *Oscinisoma alienum* (Stoneycroft Pond, *P. arundinacea,* 31.v.2000, emerged 05.vii.2000). This is the first host-plant record for *C. zetterstedti. Conioscinella zetterstedti* occurs in a range of habitats including peatlands, sedge meadows, shoreline debris, among grass roots and leaf litter and in seashore dune grasses (Wheeler 1994), suggesting that it is a generalist scavenger on plant material. Other *Conioscinella* species have a wide range of habits but many are apparently saprophagous (Ferrar 1987).

Seven species of Chloropidae (*C. zetterstedti, Elachiptera angustifrons, Elachiptera penita, Eribolus longulus, Eribolus nana, Eribolus nearcticus, Oscinisoma alienum*) were reared from a total of four stems of *P. arundinacea* infested by *A. ophiogramma.* The chloropid larvae were mostly in the lower part of the burrow excavated by the noctuid larvae, which was usually higher in the burrow.

Elachiptera angustifrons Sabrosky (Chloropidae).—One adult emerged from one stem of *P. arundinacea* infested by *Apamea ophiogramma,* along with an adult of *E. penita* and *Eribolus* spp (Stoneycroft Pond, 31.v.2000, emerged 21.vi.2000). This is the first host-plant record for *E. angustifrons.* Species of *Elachiptera* are usually considered secondary invaders of grasses and plant scavengers in general, usually in wet habitats (Valley et al. 1969b, Ferrar 1987).

Elachiptera penita (Adams) (Chloropidae).—One adult emerged from one stem of *P. arundinacea* infested by *Apamea ophiogramma,* along with an adult of *E. angustifrons* and *Eribolus* spp (Stoneycroft Pond, 31.v.2000, emerged 21.vi.2000). This is the first host-plant record for *Elachiptera penita.*

Eribolus longulus (Loew) (Chloropidae).—Adults emerged from two stems of *P. arundinacea* infested by *Apamea ophiogramma,* along with *E. nana* and *E. nearcticus* (Stoneycroft Pond, 31.v.2000, emerged 17.vi.2000 (3) and 19.vi.2000 (1)).This is the first record of this species from *Phalaris.* Three other larvae and 18 pupae, probably *Eribolus* species, died before emergence in one of the stems. Like *Elachiptera,* species of *Eribolus* are usually considered secondary invaders of grasses and other plant material in wet habitats (Ferrar 1987, Valley and Foote 1996) and *E. longulus* is apparently confined to wet open habitats dominated by sedges or grasses (Valley and Foote 1996). *Eribolus longulus* has been reared from damaged stems of *Carex* and *Scirpus,* developing flowers of *Iris,* and several genera of grasses (*Avena, Echinochloa, Glyceria, Triticum*) (Valley et al. 1969b, Valley and Foote 1996).

Eribolus nana (Zetterstedt) (Chloropidae).—Adults emerged from two stems of *P. arundinacea* infested by *Apamea ophiogramma,* along with *E. longulus* and *E. nearcticus* (Stoneycroft Pond, 31.v.2000, emerged 17.vi.2000 (1), 19.vi.2000 (1), 21.vi.2000 (1), 22.vi.2000 (1), 27.vi.2000 (1) and 30.vi.2000 (1)). This is the first record of this species from *Phalaris. Eribolus nana* has been reared from *Carex, Scirpus* and *Sparganium* L. (Sparganiaceae) (Valley et al. 1969b, Uffen and Chandler 1978).

Eribolus nearcticus Sabrosky (Chloropidae).—Adults emerged from three stems of *P. arundinacea* infested by *Apamea ophiogramma,* along with *E. longulus* and *E. nana* (in two stems), and with *Oscinisoma alienum* and *Conioscinella zetterstedti* (in a third stem) (Stoneycroft Pond, 31.v.2000, emerged 17.vi.2000 (1), 19.vi.2000 (6), 21.vi.2000 (3), 27.vi.2000 (1) and 30.vi.2000 (1)). This is the first host-plant record for *E. nearcticus.*

Lasiosina canadensis Aldrich (Chloropidae).—Two adults were reared from a culm of *C. lacustris* (Lac St. François, 16.vii.1999, emerged 17.viii.1999). Adults were swept from stands of *C. lacustris,* and of *C. aquatilis-Calamagrostis canadensis* (Michx.) Beauv. from mid-May to late October. Its relatively high abundance in October may indicate multivoltinism. This species has been reported as a secondary invader of *Carex interior, C. hystricina* Muhl. and *Scirpus cyperinus* (L.) Kunth, feeding on the decaying tissue damaged by the primary invader (Valley et al. 1969b).

Oscinisoma alienum (Becker) (Chloropidae).—One adult emerged from a stem of *P. arundinacea* infested by *Apamea ophiogramma,* along with *Conioscinella zetterstedti* and *Eribolus nearcticus* (Stoneycroft Pond, 31.v.2000, emerged 05.vii.2000). This is the first record from *Phalaris*; this species has been reared as a secondary invader from *Scirpus microcarpus* Presl. (Valley et al. 1969b).

Rhopalopterum atriceps (Loew) (Chloropidae).—Adults were reared on two occasions from *C. lacustris* (Lac St. François, 09.vii.1999, emerged 28.vii.1999 (1); same except 18.ix.1999, emerged 04.i.2000 (6), and 10.i.2000 (1)). In one case, seven adults emerged from the same stem but ten larvae were previously observed feeding deep in the culm within 5 cm of the base on rotting tissues previously attacked by a phytophagous invader. This is the first record of this species from *C. lacustris.* This species was reported feeding in shoots of *Carex comosa* Boott infested by the scathophagid *Cordilura varipes* (Walker) (Valley et al. 1969b). Most specimens were collected in June. Its higher abundance in *Carex aquatilis–Calamagrostis canadensis* stands suggest that one or both of these plants is also a host for *R. atriceps.* Rearing records of *Rhopalopterum* spp. suggest that they are all secondary invaders of herbaceous plants (Valley et al. 1969b, Armstrong et al. 1996).

Thaumatomyia obtusa (Malloch) (Chloropidae).—One adult was reared from a *C. lacustris* shoot (Lac St. François, 01.x.1999, emerged 04.i.2000). The single larva was found under the second leaf sheath 6 cm above the roots. Feeding damage possibly caused by a leaf-mining moth such as *Elachista* sp. was observed on the inner leaves and frass was present inside two of the leaves. At least three species of *Thaumatomyia* are predators of Aphidoidea (Harper 1963, Alleyne and Morrison 1977, Raspi 1996) and, despite the apparent leaf-miner damage near the *T. obtusa* larva, this species probably also preys on aphids, such as *Thripsaphis ballii,* which were abundant between the inner leaves of *Carex* at the study sites. No adults of *T. obtusa* were collected from *C. lacustris* stands.

Pullimosina pullula (Zetterstedt) (Sphaeroceridae).—One adult emerged from decaying shoots of *Scirpus fluviatilis* (Lac St. François, 07.viii.1999, emerged 01.ix.1999). Although in this case the specimen was a secondary invader and emerged along with adults of *Chaetopsis massyla* (Otitidae) from a previously attacked plant, larvae of *P. pullula* probably feed on various types of decaying vegetation. *Pullimosina pullula* is found in many types of wet decaying plant matter (Marshall 1986).

Orthacheta hirtipes Johnson (Scathophagidae).—One adult was reared from a stem of *C. lacustris* that was previously invaded, possibly by *Cordilura* sp. (Scathophagidae) or by a weevil (Lac St. François, 07.viii.1999, emerged 24.i.2000). *Orthacheta hirtipes* has been reported as a facultative predator of five *Cordilura* species, which are stem-borers of *Carex* species (Neff and Wallace 1969). This is the first record of this species from *C. lacustris.*

Coleoptera

Sphenophora costipennis (Horn) (Curculionidae).—Three adults were reared from *C. lacustris* (Lac St. François, 12.vii.1999, emerged 01.x.1999 (1); same except 23.viii.1999, emerged 08.x.1999 (1); same except 11.ix.1999 (1)). Several larvae were found in July and a few in August, within the base of the culm. Burrows examined were usually 6–7.5 cm long (rarely up to 13 cm). Numerous stems of *C. lacustris* were observed during these months with empty burrows and large exit holes close to the base, probably caused by *S. costipennis*; this species may contribute most to feeding injury of *C. lacustris* at Lac St. François and may play an important role in the colonization of Diptera secondary invaders in such sedge meadows. Previous records of this species are from *Carex comosa* F. Boott and *Scirpus validus* Vahl. (Vaurie 1951).

Sphenophora australis (Vaurie) (Curculionidae). One adult was reared from a stem of *Typha latifolia* (Lac St. François, 21.viii.1999, emerged viii.x.1999). This stem-boring species is widespread in North America. Vaurie (1951) cited *T. latifolia* as the preferred host, but also mentioned *Sparganium eurycarpum* Engelm. as a host.

Lepidoptera

Cosmopterix fernaldella Walsingham (Cosmopterigidae).—Five adults were reared from several mined leaves of *C. lacustris* (Lac St. François, 27.x.1999, emerged 09.ii.2000). Leaf-mines were conspicuous and abundant from August to October 1999. Usually several leaves on the same host plant were mined, which suggests that a single female lays eggs on many leaves of the same shoot. The larvae were sometimes observed outside of the mine, probably feeding externally on the leaves. Hodges (1978) reported that *C. fernaldella* feeds on *Carex* but did not specify a host species. *Cosmopterix clemensella* Stainton also mines the leaves of *Carex* (Hodges 1978) and an unidentified *Cos-*

mopterix sp. was reared from *Carex vesicaria* L. (Frohne 1938).

Elachista sp. (Elachistidae).—Adults were reared from leaf mines on *C. lacustris* (Lac St. François, 19.x.1999, emerged 14.iii.2000 (1); same except 27.x.1999, emerged 21.iii.2000 (1)). Infested sedges were most commonly seen in October, when larval feeding damage was more advanced. Only the basal parts of the innermost leaves were attacked, in contrast to *Cosmopterix fernaldella* and Agromyzidae that attack the upper parts of the leaves. The mines of mature larvae were usually 15–20 cm in length, usually starting within 1 cm of the culm base. The first few centimeters of the mine were narrow, brown and zigzag shaped. The upper portion was filled with white frass with the caterpillar always at the upper end of the mine. Occasionally, two mines were found in the same *Carex* stem, but on different leaves; and other shoots were simultaneously attacked by *Chlorops seminiger.* In the lab pupation occurred outside the mine in a cocoon attached to the mesh cover or bottom of the container. The immature stages and food plant are unknown for many species of *Elachista* (Braun 1948). A similar leaf mine was described for a species attacking *Diarrhena americana* Beauv. (Poaceae); that species was said to undergo a long resting period during which the early mine turns brown (Braun 1948). At least three species are known to mine *Carex,* but our biological observations indicate that the reared species is distinct from those species. Many *Elachista* species start feeding in fall; some start in spring, are dormant for the summer and resume feeding in fall; others have continuous development throughout the season (Braun 1948). The species we reared is probably of the dormant type, with two separate feeding periods.

Apamea ophiogramma (Esper) (Noctuidae).—Two adults emerged from two stems of *P. arundinacea* (Stoneycroft Pond, 31.v.2000, emerged 28.vi.2000). Larvae or pupae were seen in six shoots and several others had similar damage but were empty. Infested shoots were shorter than intact ones, with yellowish terminal leaves. Infested shoots had an entry hole 2–3 mm in diameter and 2–11 cm above the base. On two occasions, two holes were observed on the same shoot with a mass of green frass just above each hole, indicating that two caterpillars attacked the same shoot. Numerous Diptera larvae were found feeding on frass and decaying plant tissues in the six *A. ophiogramma* burrows examined; several of these were reared to adults (see above). This is the first North American rearing record of *A. ophiogramma* (J. D. Lafontaine, pers. comm.). This introduced Palearctic species was first recorded in British Columbia in 1992 (Troubridge et al. 1992) and is now also established in southern Quebec (Handfield 1999). Our specimens belong to the dark form of the species. The larvae are stem-borers of *P. arundinacea, Glyceria maxima* Hartm., *Phragmites communis* Trin. (Poaceae) and *Iris pseudacornis* L. (Iridaceae).

DISCUSSION

This study established 15 new host-plants for three phytophagous species and 12 secondary invaders, including the first host records for five chloropid species. This reflects the current lack of knowledge on the feeding habits of Diptera, particularly Chloropidae, associated with Poaceae and Cyperaceae (Ferrar 1987). Other than the rearing survey of Valley et al. (1969b) and a few studies on the life-cycle and immature stages of selected species (e.g., Rogers et al. 1991, Wearsch and Foote 1994, Valley and Foote 1996), the biology of Nearctic Chloropidae is largely unknown.

Based on rearing data and observations of infested plants, the four primary invaders recorded on *C. lacustris* (Table 1) all seem to be well established on this host. This is probably also true for *Chromatomyia fuscula* and *Apamea ophiogramma* on *P. arundinacea*; both species were repeatedly reared or observed from a sample of the host plant taken from one small stand on a single date.

There were at least three species of chloropids in each of the four stems of *P. arundinacea* examined, apparently feeding on the decaying matter inside *A. ophiogramma* burrows. This diversity of chloropid secondary invaders was unexpected and suggests that these flies may frequently be present in mixed infestations, competing for ephemeral food resources in a limited space. A similar situation probably occurs in a wide range of host plants.

One of the reasons that so little biological information is available for larval Brachycera is that emergence rates are often low when rearing flies. Many Diptera breeding in sedges and grasses probably overwinter as third-instar larva or pupa within young shoots (Nye 1958, Wallace and Neff 1971, Rogers et al. 1991). Our success in rearing flies was higher when the insects were collected in the field as a mature larva or pupa near the beginning of the warm season or at the end of it. The search for infested plants should be concentrated during these periods to increase the probability of successful rearing.

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CLADISTIC AND BIOGEOGRAPHIC ANALYSES OF *APSIL* MALLOCH AND *REYNOLDSIA* MALLOCH (DIPTERA: MUSCIDAE) OF SOUTHERN SOUTH AMERICA

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Abstract.—*Apsil* Malloch and *Reynoldsia* Malloch are genera endemic to Patagonia and southern Chile. A cladistic analysis for each genus is presented. The analysis of *Apsil* supports its monophyly on the basis of two synapomorphies, flat head and high gena. The phylogenetic relationships of *Apsil* species found are: ((*A. pennata* (*A. dilata, A. spatulata*)) (((*A. maculiventris, A. apicata*) (*A. maculipennis, A. biseta*)) *A. atripes*)). The analysis of *Reynoldsia* supports its monophyly on the basis of very long and slender palpi. The phylogenetic relationships of *Reynoldsia* species found are: ((*R. pectinata* (*R. pteropleuraris, R. rufoapicata*)) (*R. coxata* (*R. brevitarsis* (*R. aurifera, R. scutellata*)))). The cladistic biogeographic analysis of both genera shows a distribution pattern congruent with recent biogeographic reconstructions of southern South America. The distribution pattern of *Apsil* species is more restricted than that of *Reynoldsia.* By the distribution pattern found in *Reynoldsia,* the occurrence of *Reynoldsia* species on Malvinas Islands could be expected.

Key Words: *Apsil, Reynoldsia,* Muscidae, cladistic, biogeography, South America

Among the 29 recognized genera of the Coenosiini (Muscidae, Coenosiinae) (Couri and Pont 2000), *Apsil* and *Reynoldsia,* both described by Malloch (1929, 1934), are the only ones endemic to Patagonia and southern Chile. Both genera can be easily recognized with the key to the world genera of the Coenosiini (Couri and Pont 1999).

According to Hennig (1959), the cosmopolitan range of many genera is regarded as indicator of their antiquity. Skidmore (1985) called attention to the predominance of the coenosiines over other muscids both in polar regions and in the high montane equatorial regions.

All known adults of Coenosiinae are predators and are possibly so also in the larval stage. No second instar coenosiine larva has been described (except for certain *Lispe*) and probably they are all monomorphic (Skidmore 1985).

Few references to these taxa have been made in the literature since the original descriptions. Recently, Couri (1995, 1998) redescribed *Reynoldsia* and Couri (2000) revised the eight known *Apsil* species.

Our objectives are to perform a cladistic analysis of the species of *Apsil* and *Reynoldsia* and to analyze the geographic distribution patterns of the species of these genera.

Material and Methods

The cladistic analyses of *Apsil* and *Reynoldsia,* considered by Couri and Pont

(2000) as sister-groups, were made separately and were carried out using Hennig86 version 1.5 (Farris 1988), and "Tree Gardener" version 2.2 (Ramos 1997), a program designed for running Hennig86 under Windows environment. Minimum-length trees were calculated using options "ie" associated with "successive weighting." The data matrix and the characters are shown in Tables 1 and 2.

Eight species of *Apsil* were analyzed using on 22 characters, and *Reynoldsia* with its seven species was analyzed using 25 characters. Characters were polarized by the outgroup method (Watrous and Wheeler 1981, Maddison et al. 1984). The outgroups were represented by three species: *Schoenomyza armipes* Malloch 1934, *Notoshoenomyza costata* Snyder 1957 and *Spathipheromyia guttipennis* Thomson 1869. These three genera compose, together with *Apsil, Reynoldsia,* and *Schoenomyzina* Malloch 1934, a larger monophyletic group of Coenosiini, according to Couri and Pont (2000) mainly distributed in southern South America. Characters were coded as binary and multistate, the latter were considered as additive or nonadditive (characters 18 and 22 in *Apsil,* and 7 and 20 in *Reynoldsia*), depending on the availability of information on contiguity of states in the outgroups. Cladograms were made using WINCLADA (Nixon 1999, version 0.9.9 beta).

Cladistic biogeographic methods (see Morrone and Crisci 1995 for review) were used to construct taxon-area cladograms from the different taxon cladograms. A comparison of the general area cladogram was made based in some published papers.

Table 1. Data matrix and characters of the species of *Apsil* used in the analysis. 0 = plesiomorphic character states; 1 and 2 = apomorphic character states.

Outgroup	00000 00000 00000 00000 00
A. pennata	10011 00000 01000 01010 20
A. dilata	11111 00100 01010 00210 20
A. spatulata	11000 00000 01010 11210 12
A. maculiventris	11110 10120 01111 01001 21
A. apicata	11002 11010 01111 11011 02
A. maculipennis	11010 10001 10101 10100 01
A. biseta	11011 10001 11111 10100 01
A. atripes	10111 11010 00011 10000 11

1. Shape of head. [0] round, not flat; [1] flat [ci:100; ri:100; weight:10; steps:1].

2. Male: color of the pollinosity at face. [0] silver; [1] golden [ci:50; ri:50; weight:2; steps:2].

3. Shape of eyes. [0] not elongate; [1] elongate [C.I.: 33; ri:0; weight:0; steps:3].

4. Width of gena. [0] high; [1] very high [ci:33; ri: 0; weight:0; steps:3].

5. Number of frontal setae. [0] 5; [1] 4; [2] 3 [ci:40; ri:0; weight:0; steps:5].

6. Hairs at arista. [0] almost absent; [1] short hairs present [ci:100; ri:100; weight:10; steps:1].

7. Length of antennal flagellum related to pedicel. [0] twice longer or more; [1] less then twice longer [ci:50; ri:0; weight:0; steps:2] (unordered).

8. Enlargement at apex of palpi: [0] absent; [1] present. [ci:50; ri:0; weight:0; steps:2].

9. Acrostichals presutural hairs. [0] developed; [1] not developed; [2] one cilia [ci:66; ri:50; weight:3; steps:3].

10. Brown cloud at stigma in wind. [0] absent; [1] present [ci:100; ri:100; weight:10; steps:1].

11. Small dark mark in first posterior cell almost below apex of second vein. [0] absent; [1] present [ci: 100; ri:100; weight:10; steps:1].

12. Length of hind tarsus related to hind tibia. [0] much over ⅔ as long as tibia; [1] not over ⅔ as long as tibia [ci:33; ri:0; weight:0; steps:3].

13. Color of tibia. [0] brown; [1] yellow or yellowish [ci:100; ri:100; weight:10; steps:1].

14. Size of claws and pulvilli. [0] developed; [1] very reduced [ci:33; ri:0; weight:0; steps:3].

15. Width of frons at level of anterior ocellus. [0] about ⅓; [1] larger than ⅓ [ci:100; ri:100; weight:10; steps:1].

16. Antennal insertion. [0] not projected; [1] slightly projected [ci:33; ri:33; weight:1; steps:3].

17. Insertion of antenna relative to the transverse mid-line of head (head viewed from in front): [0] near; [1] a little far above. [ci:33; ri:33; weight:1; steps:3].

18. Length of lower calypter related to upper one. [0] twice longer; [1] almost the same size; [2] 1.5 times longer [ci:100; ri:100; weight:10; steps:2] (unordered).

19. Posteroventral series of bristles at fore femur related to posterodorsal series. [0] not stouter than those of posterodorsal series; [1] stouter [ci:50; ri:66; weight: 3; steps:2].

20. Brown marks at abdominal tergites 1+2, 3 and 4 abdomen. [0] two marks; [1] a unique large mark [ci:100; ri:100; weight:10; steps:1] (unordered).

21. Color of abdominal tergite 5. [0] all same color; [1] with 2 longitudinal brown marks; [2] with 2 round brown marks [ci:33; ri:20; weight:0; steps:6].

22. Marks at scutellum. [0] all same colour; [1] with 2 lateral brown lines reaching the apex; [2] with 2 lateral brown lines reaching the apex [ci:66; ri:66; weight:4; steps:3] (unordered).

←

Table 2. Data matrix and characters of the species of *Reynoldsia* used in the analysis. 0 = plesiomorphic character states; 1 and 2 = apomorphic character states; ? = missing data.

Outgroup	00000 00000 00000 00000 00000
R. pectinata	10001 12111 00011 11100 011??
R. pteropleuralis	10111 10111 01100 01011 ??010
R. rufoapicata	10111 12111 00110 01111 01011
R. coxata	11100 00001 10100 00002 10101
R. brevitarsis	11100 00001 11200 00000 100??
R. aurifera	11100 01000 10200 01110 ???10
R. scutellata	11100 00000 10201 10010 ???01

1. Shape of palpi. [0] not very long and slender; [1] very long and slender. [ci:100; ri:100; weight:10; steps:1].

2. Setulae on fronto-orbital plate. [0] numerous; [1] few and weak [ci:100; ri:100; weight:10; steps:1].

3. Setulae on parafrontale. [0] numerous; [1] few and weak [ci:50; ri:0; weight:0; steps:2].

4. Length of antennal flagellum related to pedicel. [0] twice longer or less; [1] more than twice longer [ci:100; ri:100; weight:10; steps:1].

5. Antennal insertion. [0] not projected; [1] slightly projected [ci:100; ri:100; weight:10; steps:1].

6. Width of gena. [0] not very high; [1] very high [ci:100; ri:100; weight:10; steps:1].

7. Color of pruinosity at face. [0] grey; [1] golden [2] silver. [ci:66; ri:0; weight:0; steps:3] (unordered).

8. Color of frontal triangle. [0] dark, contrasting with the ground colour; [1] not contrasting with the ground colour [ci:100; ri:100; weight:10; steps:1].

9. Length of frontal triangle. [0] short; [1] long [ci: 100; ri:100; weight:10; steps:1].

10. Marks at scutellum. [0] all same colour; [1] with 2 lateral brown lines reaching the apex. [ci:50; ri:50; weight:2; steps:2].

11. Color of knob: [0] totally brown; [1] yellow and brown. [ci:100; ri:100; weight:10; steps:1].

12. Acrostichals presutural hairs. [0] developed; [1] not developed [ci:50; ri:0; weight:0; steps:2].

13. Disc of katepisternum: [0] with many ground-setulae; [1] with few ground-setulae; [2] almost bare [ci:66; ri:66; weight:4; steps:3].

14. Number of humeral bristles. [0] 2 or 3; [1] more than 3 [ci:50; ri:0; weight:0; steps:2].

15. Number of setae on median third of anteroventral surface of hind tibia: [0] 2; [1] 3 [ci:50; ri:0; weight: 0; steps:2].

16. Number of setae on median third of anterodorsal surface of hind tibia: [0] 2 or 3; [1] 4 [ci:50; ri:0; weight:0; steps:2].

17. Number of setae on median third of anterodorsal surface of mid tibia: [0] 2; [1] 3 [ci:50; ri:66; weight:3; steps:2].

18. Number of supramedian setae on posterior surface of mid tibia: [0] 1; [1] 2 [ci:33; ri:0; weight:0; steps:3].

19. Color of fore femur. [0] all same colour, dark brown; [1] dark brown, yellow at apex [ci:50; ri:66; weight:3; steps:2].

The distribution data of *Apsil* and *Reynoldsia* were taken from Malloch (1929, 1934) and (Couri 1995, 1998, 2000) (Appendices 1, 2).

RESULTS AND DISCUSSION

Phylogenetic analysis.—Only one tree was found for each analysis, with a length of 137 and 162, a consistency index (C.I.) of 88 and 91 and a retention index (R.I.) of 90 and 93, respectively for *Apsil* (Fig. 1) and *Reynoldsia* (Fig. 2).

The analysis of *Apsil* supports its monophyly on the basis of the following shared synapomorphies: flat head, high gena and four frontal setae. The most basal dichotomy divides the genus into two groups: (*A. pennata* + *A. dilata* + *A. spatulata*) and (*A. maculiventris* + *A. apicata* + *A. maculipennis* + *A. biseta* + *A. atripes*), the latter defined by two synapomorphies; presence of short hairs at arista and width of the frons larger than ⅓ of head. *Apsil biseta* and *A. maculipennis* are the only *Apsil* species that show a brown cloud at the stigma in the wing, a small dark mark in the first posterior cell almost below the apex of the second vein, and the calypters almost of same size. Malloch (1934) mentioned the remarkable morphological similarity of these two species.

The analysis of *Reynoldsia* supports its monophyly on the basis of very long and slender palpi. The most basal dichotomy di-

←

20. Color of hind femur. [0] dark brown, yellow at apex; [1] dark brown on basal half and yellow at apical half; [2] totally dark brown [ci:100; ri:100; weight:10; steps:2] (unordered).

21. Sternite 5 arms. [0] large [1] medium [ci:100; ri: 100; weight:10; steps:1].

22. Width of cercal plate. [0] large; [1] thin [ci:100; ri:100; weight:10; steps:1].

23. Aedeagus apodem. [0] shorter and larger; [1] longer and thinner [ci:50; ri:0; weight:0; steps:2].

24. Bristles on sternite 8 of ovipositor. [0] long and fine; [1] short and strong [ci:50; ri:50; weight:2; steps: 2].

25. Shape of epiproct. [0] not divided; [1] divided [ci:33; ri:0; weight:0; steps:3].

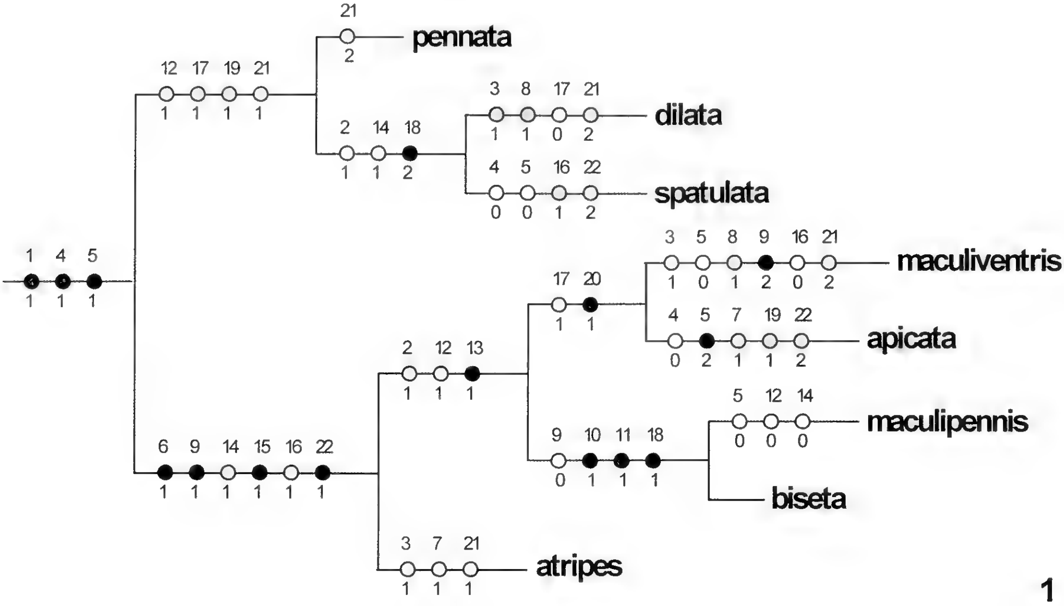


Fig. 1. Cladogram depicting the phylogenetic relationships among the species of *Apsil.* Length: 137; C.I.: 88; ri: 90. Black boxes, synapomorphies; gray boxes, homoplasies; clear boxes, reversals.

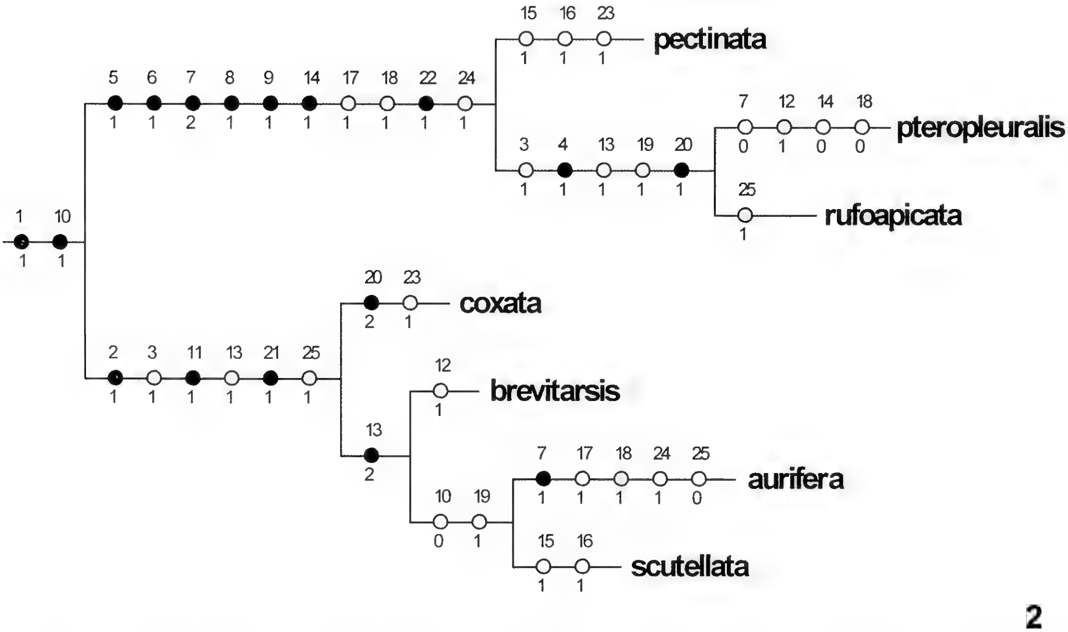
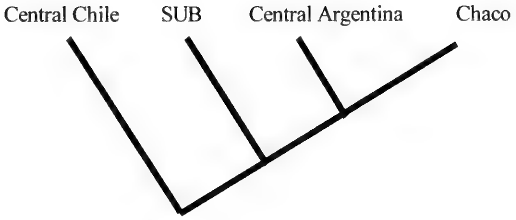
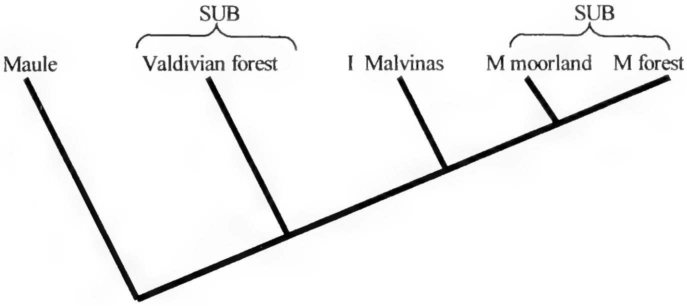


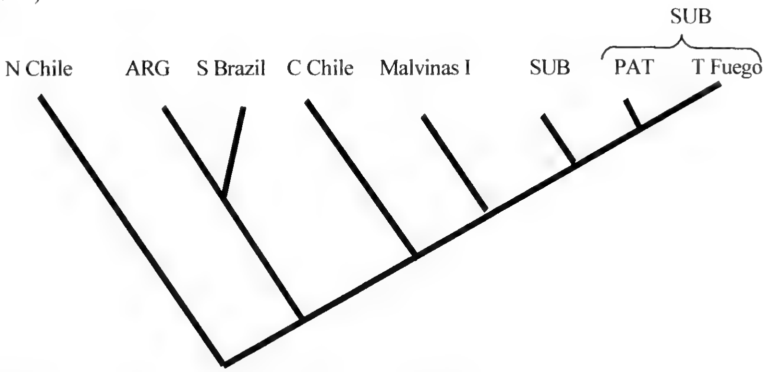
Fig. 2. Cladogram depicting the phylogenetic relationships among the species of *Reynoldsia.* Length: 162; C.I.: 91; ri: 93. Black boxes, synapomorphies; gray boxes, homoplasies; clear boxes, reversals.



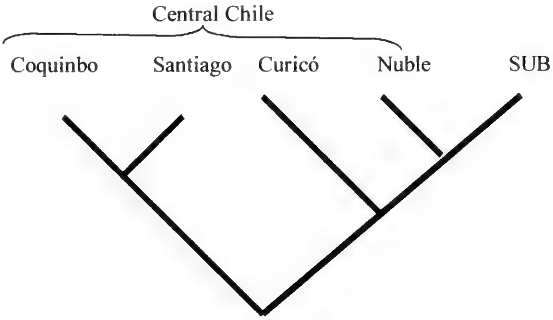
a) Morrone (1993)



b) Morrone et al. (1994)



c) Amorim & Pires (1996) [based on Morrone (1993) and Morrone (1994)].



(d) Morrone et al. 1997

3

Fig. 3. Biological area cladogram for southern South America. C = Central; I = Isles; M = Magellanic; N = North; PAT = Patagonian province; S = South; SUB = Subantarctic province; T = Tierra del.

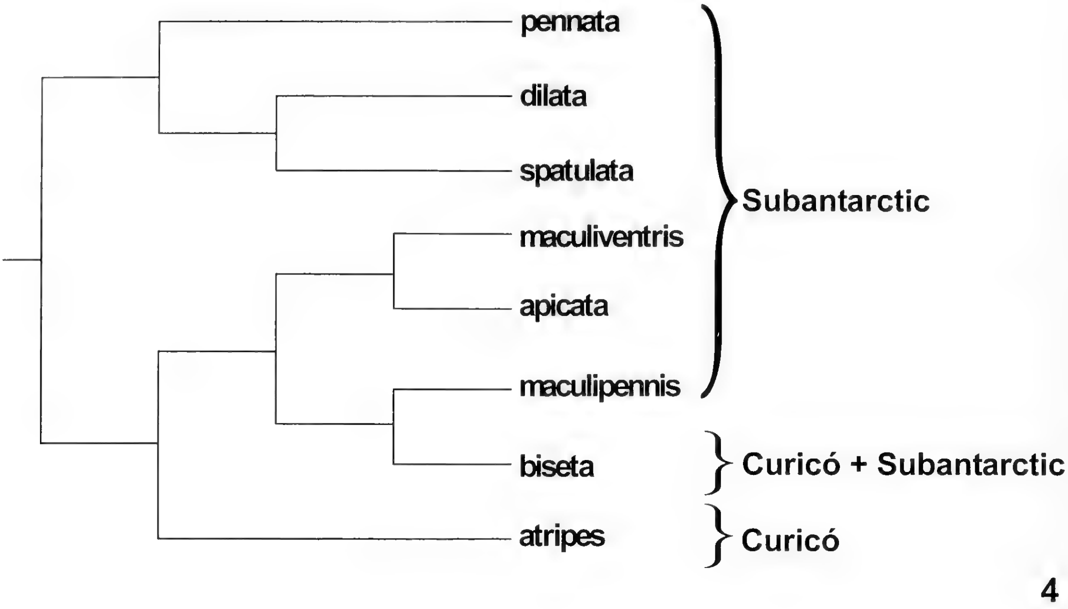


Fig. 4. Taxon-area cladogram of species of *Apsil.*

vides the genus into two groups: (*R. pectinata* + *R. pteropleuralis* + *R. rufoapicata*) and (*R. coxata* + *R. brevitarsis* + *R. aurifera* + *R. scutellata*). The first group is defined by five synapomorphies (the slightly projected antennal insertion, the very high width of the gena, the color of the frontal triangle not contrasting with the ground color, the long frontal triangle, and a thin cercal plate) and the second one by three (presence of few and weak setulae on the fronto-orbital plate, the brown and yellow knob, and sternite 5 arms medium in width).

Biogeographic analysis.—The biogeographical patterns of distribution of Muscidae are scarcely known in the world. For the Neotropical Region, only Hennig (1965) and more recently Carvalho (1999) analyzed patterns of distribution of Muscidae species in South America with a dispersalist and a cladistic view, respectively; however, in the southern part of this continent, below 30°S latitude but including the Andean highland northern of this latitude (Kuschel 1969, Cabrera and Willink 1973, Crisci et al. 1991, Morrone 1993, Morrone et al. 1994, Morrone and Lopretto 1994, Amorim and Pires 1996), there are no historical biogeographic studies with Muscidae.

The biogeographical patterns of some endemic taxa in southern South America have been recently studied with cladistic biogeographic methods (Crisci et al. 1991; Morrone 1993, 1994; Morrone et al. 1994, 1997). Selected biological area cladograms proposed for southern South America are shown in Fig. 3.

The taxon-area cladograms of *Apsil* (Fig. 4) and *Reynoldsia* (Fig. 5) were compared with those patterns found (Fig. 3) and shown to be congruent with those biogeographic reconstructions.

The distribution pattern of *Apsil* species is more restricted than *Reynoldsia* species. *Apsil atripes* is the only species (Fig. 4) exclusively occurring to the north of the subantarctic area corresponding broadly to the Curicó area of central Chile of Morrone et al. (1997). They tried to explained the patterns of central Chile and their study supports a vicariant explanation of the patterns analyzed.

All *Reynoldsia* species are spread in the

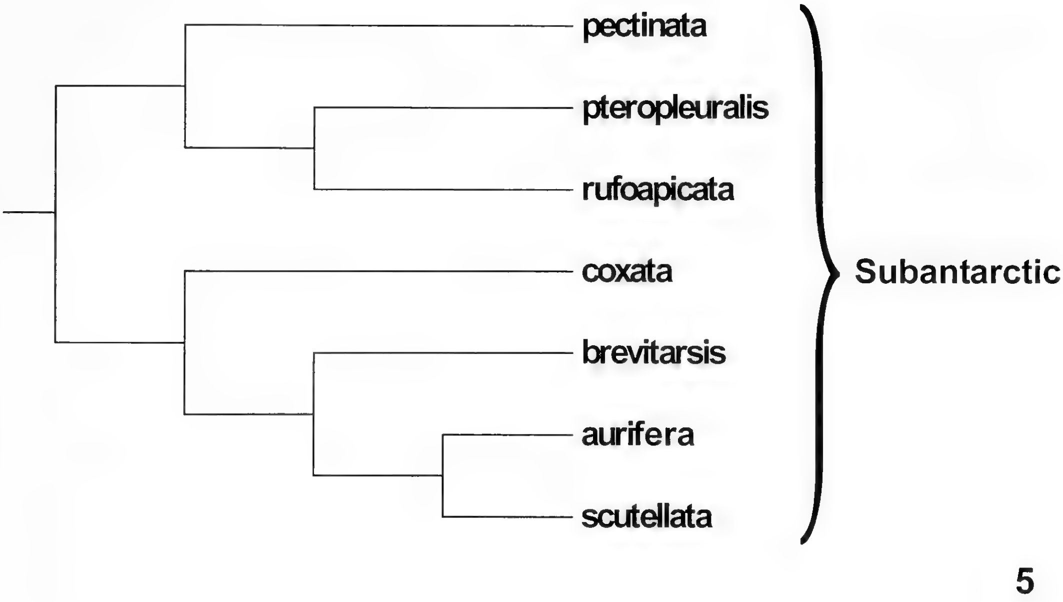


Fig. 5. Taxon-area cladogram of species of *Reynoldsia.*

subantarctic area, with only *Reynoldsia pectinata* occurring in Tierra del Fuego (Appendix 2). By the distribution pattern found in *Reynoldsia,* compared with the biological reconstruction of southern Chile by Morrone et al. 1994 (Fig. 3b), it could be expected that undescribed species of *Reynodsia* occur in Malvinas Islands, which are part of the subantarctic area, here understood as a major monophyletic area (see Amorim and Pires 1996).

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APPENDIX 1

Localities of species of *Apsil* in South America including latitude and longitude. Abbreviations: E = East, m = meters, k = kilometers, v. valley.

Apsil apicata Malloch 1934.—ARGENTINA: Lake Correntoso (40°44′S, 71°40′W); San Carlos de Bariloche (41°11′S, 71°23′W). CHILE: Casa Pangue (41°03′S, 71°52′W).

Apsil atripes Malloch 1934.—CHILE: Rio Colorado (33°04′S, 71°39′W); Curicó (34°59′S, 71°14′W); Talca, 800 m (35°20′S, 71°46′W); Concepción (San Rosendo) (37°16′S, 72°43′W).

Apsil biseta Malloch 1934.—ARGENTINA: Volcán (36°26′S, 67 °09′W); San Carlos de Bariloche (41°11′S, 71°23′W). CHILE: Las Cabras, 1480 m (34°18′S, 71°19′W); Angol (37°47′S, 72 °45′W); Malalcahuello (4–14 k E., 1080–1570 m.) (38°27′S, 71°35′W); Curacautin (38°28′S, 71°52′W); Villarica, 1250 m (39°15′S, 72°30′W); Coihaique (v. of Simpson river) (45°35′S, 72°08′W).

Apsil dilata Malloch 1934.—ARGENTINA: San Carlos de Bariloche (41°11′S, 71°23′W). CHILE: Ancud (41°53′S, 73°50′W); Puntra (42°07′S, 73°49W); Castro (42°30′S, 73°46′W).

Apsil maculipennis Malloch 1934.—ARGENTINA: Volcán (36°26′S, 67°09′W); Lake Correntoso (40°44′S, 71°40′W); Puerto Blest (41°02′S, 71°59′W). CHILE: Malalcahuello (12 k E, 1080 m) (38°27′S, 71°35′W); Curacautin (38°28′S, 71°52′W); Villarica (39°15′S, 72°30′W); Osorno (40°35′S, 73°14′W); Parque Nacional Puyehue (40°40′S, 72°37′W); Coihaique (v. of Simpson river) (45°35′S, 72°08′W).

Apsil maculiventris Malloch 1929.—CHILE: Perales (36°40′S, 72°39′W).

Apsil pennata Malloch 1934.—ARGENTINA: San Carlos de Bariloche (41°11′S, 71°23′W). CHILE: Casa Pangue (41°03′S, 71°52′W).

Apsil spatulata Malloch 1934.—ARGENTINA: San Carlos de Bariloche (41°11′S, 71°23′W). CHILE: Peulla (41°06′S, 72°02′W); Puntra (42°07′S, 73°49′W).

APPENDIX 2

Localities of species of *Reynoldsia* in South America including latitude and longitude. Abbreviation: m = meters.

Reynolsia aurifera Bigot 1885.—ARGENTINA: Lolog (40°05′S, 71°19′W). CHILE: Casa Pangue (41°03′S, 71°52′W); Ancud (41°53′S, 73°50′W).

Reynolsia brevitarsis Malloch 1934.—ARGENTINA: San Carlos de Bariloche (4°11′S, 71°23′W); Lake Gutierrez (41°11′S, 72°23′W).

Reynolsia coxata Malloch 1934.—ARGENTINA: Lolog (40°05′S, 71°19′W); San Carlos de Bariloche (41°11′S, 72°23′W).

Reynolsia pectinata Malloch 1934.—ARGENTINA: Rio Grande (53°47′S, 67°42′W); Estancia Viamonte (54°02′S, 67°22′W). CHILE: Punta Arenas (53°09′S, 70°55′W).

Reynolsia pteropleuralis Malloch 1934.—ARGENTINA: San Martín de los Andes (40°10′S, 71°21′W); Nahuel Huapi (41°03′S, 71°12′W); CHILE: Perales (36°40′S, 72°39′W).

Reynolsia rufoapicata Malloch 1934.—ARGENTINA: San Martín de los Andes, 1500 m (40°10′S, 71°21′W); Lake Correntoso (40°44′S, 71°40′W); San Carlos de Bariloche (41°11′S, 71°23′W); Puerto Blest (41°02′S, 71°50′W).

Reynolsia scutellata Malloch 1934.—CHILE: Angol (37°47′S, 72°45′W); Cerro Nahuelbuta, 650 m (37°48′S, 73°04′W); Galvarino (38°24′S, 72°47′W).

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DESCRIPTION OF A NEW TORTRICID PEST (LEPIDOPTERA: TORTRICIDAE: OLETHREUTINAE) OF LITCHI (*LITCHI CHINENSIS*) IN FLORIDA, WITH A REVIEW OF TORTRICID PESTS OF LITCHI WORLDWIDE

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Abstract.—The adult, larva, and pupa of ***Crocidosema litchivora*** **Baixeras, new species**, are described and illustrated; details of the life history are presented. Since 1993, an increase in the abundance of *C. litchivora* in southern Florida has resulted in significant damage to commercially grown litchi (*Litchi chinensis* Sonnerat; Sapindaceae). The larvae feed on the inflorescences and buds of the host plant, significantly reducing crop yield. Owing to the absence of records of *C. litchivora* prior to 1992, it is likely that this Neotropical species is a relatively recent arrival in southern Florida. A list of tortricid pests of litchi worldwide is presented.

Key Words: *Crocidosema, Litchi chinensis,* pest species, new record, species introduction, Caribbean

Litchi chinensis Sonnerat (Sapindaceae) is a large evergreen tree native to China. The fruit, referred to as lychee, leechee, or litchi, has long been a favorite in southeastern Asia; over the last decade it has gained popularity in the United States. In the contiguous states, *L. chinensis* is grown commercially only in tropical southern Florida, where growers harvested 1.37 million pounds (0.63 million kg) in 1996, valued at $2.75 million (Stanley 1998).

The small but growing litchi industry in southern Florida was nearly destroyed in 1992 by hurricane Andrew. Subsequently, the acreage planted in litchi increased significantly; some of the new plant material was imported from Hawaii. Starting in about 1993, larvae of a tortricid moth became a pest in Florida orchards, and in 1996–1997, this species inflicted damage to litchi resulting in as high as 40% crop loss in some places. In 1997, examples of the moth were sent to the Systematic Entomology Laboratory, USDA, for identification. Although morphologically similar to the lantana flower-cluster moth (*Crocidosema lantana* Busck), which is reported to feed on litchi in the Hawaiian Islands (Zimmerman 1978), detailed studies revealed that the Florida specimens represented an undescribed species. The purposes of this paper are to present descriptions and illustrations of the new species, provide details on its biology, and briefly review tortricid pests of litchi worldwide.

MATERIALS AND METHODS

Systematics.—Specimens of the new *Crocidosema* species were collected as larvae from infested litchi trees (described below) and as adults by black-light collecting in southern Florida. Depositories are abbreviated as follows: BMNH, The Natural History Museum, London, England; IFAS, University of Florida, Institute of Food and Agricultural Services, Gainesville, Florida, USA; INBio, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; MEM, Mississippi Entomological Museum, Mississippi State, Mississippi, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; VBC, Vitor Becker personal collection, Planaltina, Brazil. Dissection methodology follows that summarized in Brown and Powell (1991). Forewing measurements were made with an ocular micrometer mounted in a dissecting microscope. Terminology for wing venation and genitalic structures follows Horak (1984); terminology for larval features follows Brown (1987). Abbreviations and symbols are as follows: FW = forewing; HW = hindwing; DC = discal cell; n = number examined; ca. = circa (approximately); $\bar{x}$ = mean; bl. = blacklight.

Biology.—Newly formed litchi leaf flushes with no evidence of Lepidoptera larvae or eggs were marked and checked daily at a single site in Dade County, Florida, from 30 March to 15 April 1998. Upon discovery of newly oviposited eggs, apical and lateral buds were collected and brought into the laboratory for further inspection. The infested buds were placed individually in 3-ml vials held at 22 ± 3°C and 75% relative humidity and observed daily until the egg chorion began to darken, indicating the development of the embryo to an advanced stage. The infested buds then were transferred to 30-ml plastic cups containing synthetic diet (Robinson et al. 1977). Eggs were observed daily for eclosion. A subsample of developing larvae were checked daily for pupation, and pupae were checked daily for adult emergence and sex determination. Representative examples of larvae were collected daily and preserved in 75% ethanol. Width of larval head capsules of all instars was measured for 106 individuals. Three newly emerged females and two males were held at 22 ± 3°C, 80% relative humidity, and 12:12 L:D in a 30 × 30 × 30 cm plexiglass cage with water and honey and litchi leaf flushes as a potential oviposition substrate. Leaf flushes were examined daily for evidence of eggs. This experiment was repeated 5 times.

RESULTS

Systematics

Crocidosema litchivora Baixeras, new species

(Figs. 1–6)

Diagnosis.—*Crocidosema litchivora* is similar to *C. lantana* Busck 1910, *C. longipalpana* (Möschler 1890), *C. calvifrons* (Walsingham 1892), and several undescribed species in the shared possession by males of strongly upturned labial palpi, with an extremely long second segment, and modified scaling on the convex frons. A distinctive male hairpencil extending from the posterior notal hindwing process to the abdomen is shared by *C. litchivora* and *C. lantana.* Although forewing pattern is similar in the latter two species, *C. lantana* always has reduced green suffusion and hence a more defined pattern, allowing superficial separation of the two in well preserved specimens. The layered sex scales beneath the costal fold of the forewing are dark brown in *C. litchivora* and silvery in *C. lantana.* The scales of the hairpencil from the posterior notal hindwing process are slightly different between the two: in *C. lantana* they are clubbed and thickened distally, whereas in *C. litchivora* they are piliform. The lateral pockets in the abdomen that receive the scales also are different between the two: in *C. lantana* the sclerotized areas are complex, surrounded by an extensive

Figs. 1–2. Adults of *Crocidosema litchivora.* 1, Male paratype. 2, Female paratype.

membranous region, and the pocket is covered by broad, non-deciduous scales; in *C. litchivora* the structure is comparatively reduced, with no membranous region, and lacks broad scales. Male and female genitalia are distinct as well. *Crocidosema lantana* lacks the pointed process on the distal ventral part of the sacculus, and the entire cucullus is curved upward. In the female genitalia the sterigma is pentagonal in *C. lantana,* with a small but evident dorsal microsclerite in the junction between the sterigma and the ductus bursae. This sclerite, which strongly stains by fuchsin acid and is 70–80μ in length, also is present in *C. litchivora,* but much more reduced (25–50 μ) and ill defined. The pair of irregularly rounded, densely scaled pockets on the seventh abdominal sternite are opened posteriorly in *C. lantana* and relatively closed in *C. litchivora*; in the latter there is a lateral tooth in each pocket that is lacking in *C. lantana.*

Description.—Male: *Head:* Antennal cilia approximately 0.5 times width of flagellomere. Labial palpus conspicuously elongate, strongly upturned, extending beyond top of head in resting position, tan, with brown and orange scales. First segment with basal third having dorsal margin curved and ventral margin forming approximate right angle, apical two-thirds extending forward in parallel axis of body, apex articulating with second segment at 90° angle; second segment long, ca. 2 times that of first, and 3 times that of third, basal third slightly curved, remainder straight and directed dorsally; third segment straight, short. Length of organ of vom Rath equal to approximately 0.25 length of segment; opening of organ in apical position. Proboscis developed, unscaled. Frons concave, clothed by small, charcoal black to olivaceous, appressed scales; scales aligned from eyes to a narrow vertical ridge at middle of frontoclypeus; ridge protruding ventrally in a group of erect longer scales and dorsally between antennae in a broad row of scales. Vertex anteriorly with overhanging tuft of blackish brown and gray scales between compound eyes; ocelli and chaetosemata well developed; tuft of erect dark brown to whitish long scales from lateral posterior part of vertex to occiput surrounding eyes. *Thorax:* Smooth-scaled, dark brown to mostly black dorsally; tegula covered by dull dark brown, sometimes yellowish, simple scales; mesonotum and metanotum covered by elongate glossy dark brown scales; scales erect on metascutum; pleural and sternal portions of thorax light brown to yellowish. Legs unmodified. Forewing (Fig. 1): Length 4.5–5.2 mm ($\bar{x}$ = 4.9; n = 5). Costal fold large, well defined, extending at least 0.45 length of FW and 0.66 distance between base of FW and point where R_1 meets costa; basal portion of R-stem obsolete; R_4 and R_5 stalked for more than half of their length with R_4 extending to costa and R_5 to termen; M-stem and chorda ill-defined if present; discal cell at least 0.7 times length of wing; M_1 and M_2 straight; M_2, M_3, and CuA_1 approximate at base with M_3 and CuA_1 parallel and curved; CuP atrophied except in distal portion; anal loop equal to 0.33 length of 1A+2A. Upperside mostly mottled black, gray, and reddish brown, with large areas of green; space between Sc and basal portion of Cu-stem covered by a layer of smooth, small dark brown scales within costal fold; costal fold enclosing a strongly developed row of white petiolate sex scales along Sc; ground color brown to reddish brown; costa with two ill defined strigulae between base of wing and Sc on distal half of costal fold; two strigulae between Sc and R_1, more basal less distinguishable; three distinct strigulae between veins R_1–R_2, R_2–R_3, and R_3–R_4 respectively; three silvery striae extending from strigulae, confluent to termen between R_4 and M_1; termen without strigulae; fasciae poorly defined; basal and subfasal fasciae fused, dark brown from costa to A1+A2, yellowish white from A2 to dorsum; median fascia dark brown, extending from costa to CuA_2, broader and darker on discal cell; postmedian fascia disjunct, with a conspicuous dark spot between R_5 and M_1 immediately anterior to ocellus, extending to termen in a narrow line from M_1 to intervening space between CuA_1 and CuA_2; subterminal fascia represented by a spot on costa; apical spot between R_4 and R_5 as a small, but distinctive group of dark brown to black scales; ocellus present, green to yellowish green with strong silvery suffusion and four small, sometimes indistinct, fascial dark brown spots; green to yellowish-green area from outer margin of subbasal fascia to tornus on dorsum. Fringe mostly green; brown in apical region. Underside brown, with four white strigulae from Sc to R_4; area of wing overlap whitish. Hindwing: Costa with basal 0.66 expanded to form broadly rounded lobe underlying forewing, narrowed before Sc+R_1; Rs and M_1 stalked; Rs extending to costa near apex, M_1 to termen; M_2 and M_3+CuA_1 arising from same point; M_3 and CuA_1 stalked; upperside uniformly grayish brown, except area of forewing overlap anterior to Sc+R_1 densely covered by silvery scales; 3 rows of modified sex scales on wing: (1) cubital pecten slightly developed consisting of a sparse row of slender elongate, brownish scales along CuP; (2) a denser row of stiff, somewhat erect tan scales along 2A in anal loop that presumably connects with erect scales on metascutum; (3) a rather large patch of long, silky scales between inner margin and 3A, denser at wing base and progressively less dense in distal half to wing margin. Fringe concolorous with remainder of hindwing. Underside of hindwing uniformly light brown. A dense hairpencil of long pale orange scales arising from posterior notal wing process, extending into a pocket of specialized scales on dorsolateral portion of second abdominal segment, emerging again from abdominal pocket on third abdominal segment. *Abdomen:* First, second, and third pleural membranes strongly modified into a series of three extended sclerotized plates; plates slightly concave and corrugated, forming depressions on first, second, and third segments, concealed by large, flat, somewhat erect, specialized scales; first three abdominal tergites covered with small dark brown sex scales; remainder light brown to yellowish. *Genitalia* (Fig. 3): Uncus short, wider at base, subtriangular, ca. 0.5 length of socius, finely setate dorsally, rounded apically. Socius well developed, crescent-shaped. Anal tube with two longitudinal

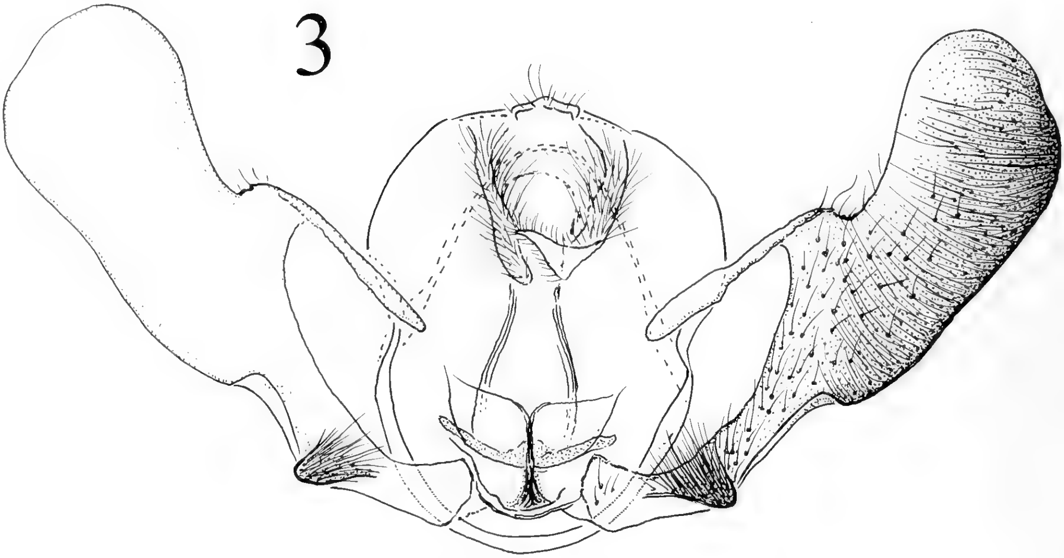

Fig. 3. Male genitalia of *Crocidosema litchivora,* valvae spread, aedeagus in situ.

ventrolateral sclerotized bands that basally connect with the two lateral arms of anellus. Valva upturned; costa with conspicuous notch approximately 0.5 distance from base to apex. Sacculus short with distinct, swollen, densely setose pointed ventral process approximately 0.20 distance from base to apex. Cucullus densely setose from neck of valva to apex. Ventral edge slightly thickened before apex. Aedeagus simple, nearly straight, with dense fascicle of 10–15 slender cornuti; attached to tegumen at base of gnathos and anal tube by a pair of slender lateral arms.

Female: FW length 4.7–5.6 mm ($\bar{x}$ = 5.0; n = 10) (Fig. 2). Similar to male, with following exceptions: antennal cilia less than 0.1 times width of flagellomere; labial palpus weakly upturned, unmodified; frons brown, convex. Mesonotum concolorous with basal and subbasal fasciae in forewing; metanotum concolorous with hindwing upperside; no erect scales on metascutum. Forewing without costal fold; four evident strigulae and striae basal to Sc; basal and subbasal fasciae poorly developed; median and postmedian fasciae slightly more developed than in male; no specialized sex scaling or hairpencil on wings or posterior notal hindwing process. First three abdominal segments unmodified, lacking sex scales. *Genitalia* (Fig. 4): Papillae anales simple, slender. Sterigma forming a slightly sclerotized subtriangular plate projected laterally and posteriorly; bearing 10–15 long setae arranged symmetrically and obliquely; sterigma forming an anterior funnel-shaped region leading to ostium. Sternite of sixth segment with a pair of irregularly rounded, densely scaled pockets with one lateral conspicuous tooth in each one. Junction of ostium and ductus bursae with small, irregularly shaped dorsal sclerite, most easily seen if ductus removed from sterigma. Ductus bursae moderately long, broadened near junction with corpus; membranous in anterior 0.33, with strongly sclerotized plate in following 0.33, and membranous in posterior 0.33. Ductus seminalis arising from dorsal position in middle of sclerotized plate. Corpus bursae pyriform, with a pair of long, curved, bladelike signa; a curved patch of short spines near junction of corpus and ductus that surrounds anteriorly a slightly developed lobe.

Larva (Fig. 5). Based on 3 last instars. *General:* Length 11 mm. Head pale orange yellow, with a dark brown genal bar and

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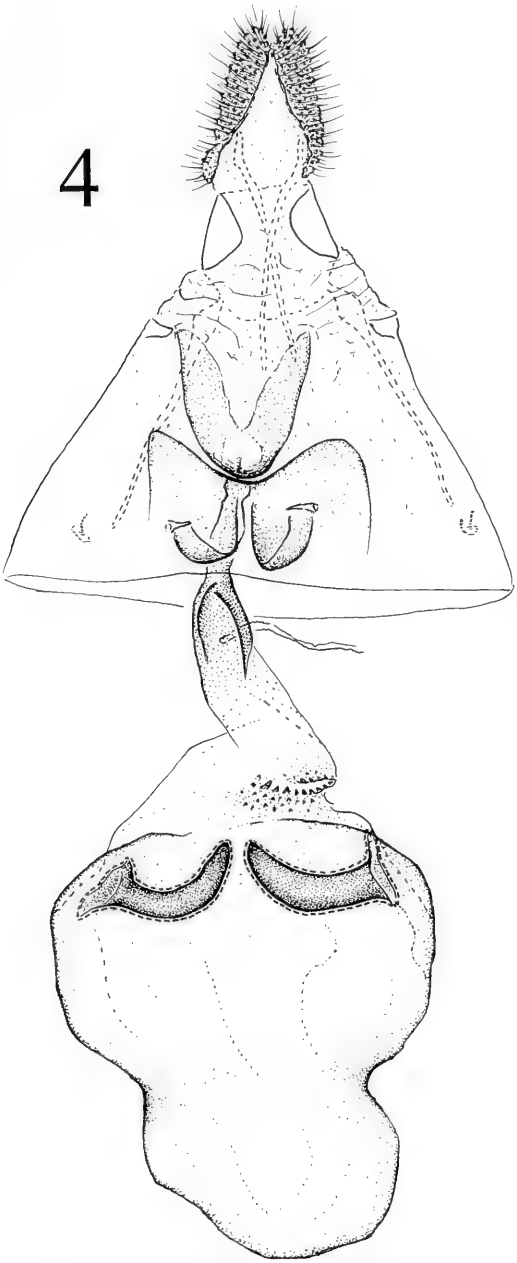

Fig. 4. Female genitalia of *Crocidosema litchivora.*

dark patch in stemmatal region; prothoracic and anal shields yellow to tan; body white to dingy grayish white, with well-defined, pale grayish brown pinacula contrasting with body color (absence of spiculae on pinacula enhances contrast); body covered with short, fine spiculae; spiracles on T1 and A8 nearly equal in size, approximately 1.3 times diameter of those on A1–7. *Head:* Frons extending ca. 0.7 to occipital foramen; stemmata arranged in a semicircle except for S5; S2 slightly smaller in diameter. *Thorax:* Prothorax with trisetose L-group on well defined pinaculum, L1 slightly closer to L2 than to L3; meso- and metathorax with D1s and D2s on same pinaculum, arranged nearly vertically. *Abdomen:* SD2 either without distinct pinaculum or on narrow extension of large SD1 pinaculum; spiracles round, larger than base (or socket) of SD1 setae on A1–7; SD1 pinaclum on A8 large, curved along posterior edge to accommodate spiracle; SV group on 1, 2, 7, 8, 9 always 3:3:2:2:2; D1 and SD1 on same pinaculum on A9; L3 on same pinaculum as L1 and L2 on A9; distance between Vs on A9 slightly greater than distance between Vs on A8 and A7; anal fork well developed, with 5–6 elongate teeth. Crochets 35–38 in a biorinal circle; anal crochets 21–24 in a continuous band.

Pupa (Fig. 6). Based on a single female. Typically olethreutine; head without projection; no conspicuous sculpturing; dorsum of thorax with posterior-projecting, mesal lobe; abdomen with 2 rows of spines dorsally on A2–7, spines of posterior row smaller, more numerous; anterior row on A4–7 extends from spiracle to spiracle; single row of strong spines on A8–9. Cremaster poorly developed, extremely short, blunt, ending in row of strong spines.

Type material.—Holotype ♂: USA: FLORIDA: Dade Co. 6 km NW Homestead, 20 March 1998, bl. (J. Brown & J. Peña, USNM). Paratypes: 1♂, same data as holotype (genitalia slide number 89828); 1♂, Florida, Homestead, November 1997, ex-litchi (genitalia slide number 88652); 7♀, same data as holotype; 2♀, same data as holotype, but 20/23 March 1998. All paratypes deposited in USNM.

Additional material examined.—USA: Florida, Dade Co., Homestead, 3♂, 2♀, 15-I-1992, as larvae on *Litchi chinensis,*

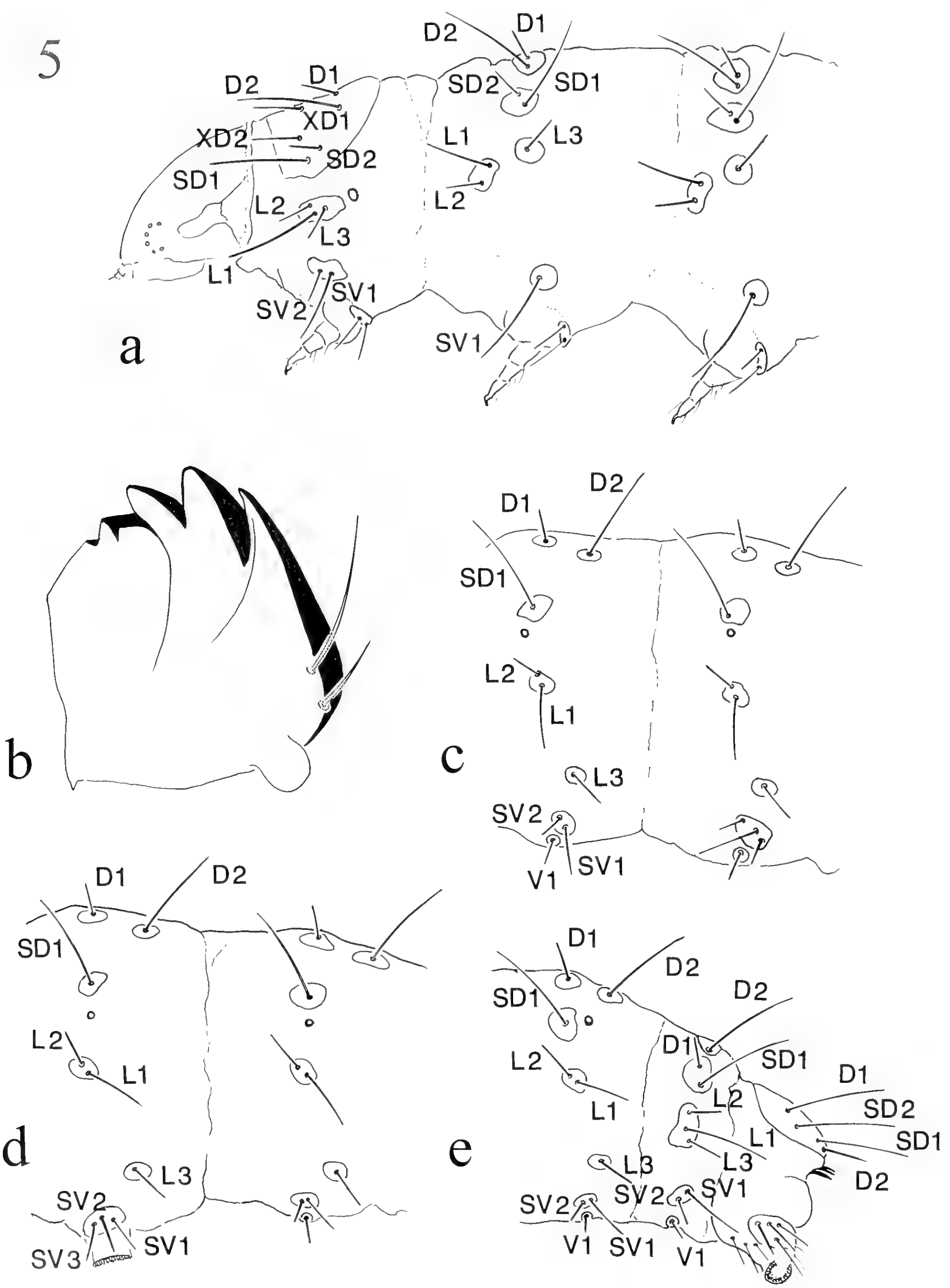

Fig. 5. Larva of *Crocidosema litchivora.* a, Head, T1–3. b, mandible. c, A1–2. d, A6–7. e, A8–10.

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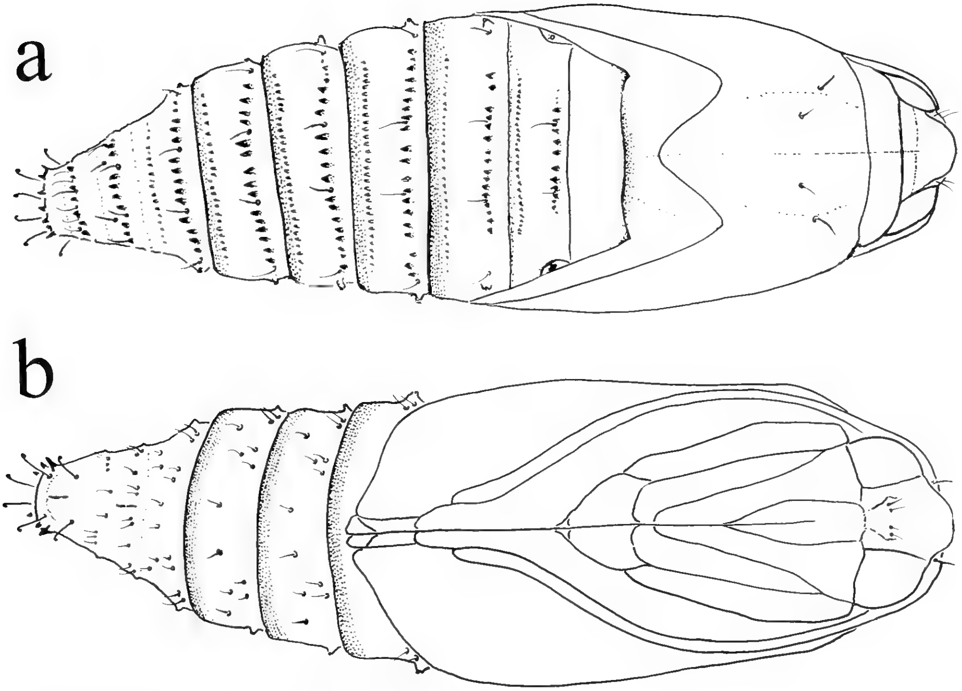

Fig. 6. Pupa of *Crocidosema litchivora*. a, Dorsum. b, Venter.

emerged 21-II/9-III-92 (J. Pena, IFAS), 1♂, 25-II-1992, 1♂, 25-II-1992, both as larvae on *Eriobotrya japonica* (R. Duncan, IFAS), 1♀, 21-I-1992, on *Clausena lansium* (R. Duncan, IFAS), 5♂, 10♀, 5-XII-1996 as larvae on *Litchi chinensis* buds (A. Catineiras, IFAS), 2♂, 3♀, XI-1997, ex-Litchi (J. Pena, USNM); Homestead, 1♂, 3♀, November 1997, as larvae on *Litchi chinensis*; 6 km NW Homestead, 1♀, 20 March 1998; 1♀, 20/23 March 1998; 4♂, 3♀, October 1998 (USNM). BRAZIL: Planaltina, Distrito Federal, 1000 m, 1♂, 15 September 1984 (V. Becker, VBC). COSTA RICA: Province of San José, P.N. Braulio Carrillo, Estación Carrillo, 700 m, 1♂, July 1990 (INBio); Province of Limón, P. N. Tortuguero, Cerro Tortuguero, 0–120 m, 1♀ April 1991, 1♂ June 1991 (INBio); Province of Limón, Sector Cerro Cocori, Fca. de E. Rojas, 150 m, 1♀, November 1990, 1♂ December 1991 (INBio); Province of Guanacaste, P. N. Guanacaste, 9 km S Santa Cecilia, Estación Pitilla, 700 m, 1♂, 23–26 June 1993 (INBio). DOMINICAN REPUBLIC: Province of Dajabon, 13 km S Loma de Cabrera, 400 m, 2♂, 20–22 May 1973 (USNM); Province of La Vega, Hotel Montana, 10 km NE Jarabacoa, 520 m, 1♂, 28 May 1973 (USNM). JAMAICA: Kingston, St. Andrew, 1♂, 12 March 1966 (S. S. & W. D. Duckworth, USNM). PUERTO RICO: Centro Vacacional Monte del Estado near Maricao, 650 m, 1♀, 1–9 March 1971 (USNM). VENEZUELA: Auyan Tepui, Camarata, 1♂, 4–17 August 1974 (B. V. Ridout, BMNH).

Etymology.—The species name is derived from the host plant genus.

Comments.—*Crocidosema litchivora* belongs to a group of Neotropical species that includes *C. lantana, C. longipalpana, C.*

Table 1. Duration of immature stages of *Crocidosema litchivora*.

	n	Days ($\bar{x}$ ± SD)
Egg	40	4 ± 0.4
1st instar	26	2 ± 0.8
2nd instar	17	3 ± 1.3
3rd instar	19	2 ± 1.0
4th instar	21	2 ± 1.0
5th instar	13	2 ± 0.5
6th instar	10	2 ± 0.9
Larva total	40	18 ± 1.1
Pupa	40	11 ± 0.9

Table 2. Head capsule widths of *Crocidosema litchivora*.

Stadium	n	Width in mm ($\bar{x}$ ± SD)
1st instar	26	0.21 ± 0.03
2nd instar	17	0.32 ± 0.03
3rd instar	19	0.56 ± 0.16
4th instar	21	0.73 ± 0.14
5th instar	13	0.97 ± 0.09
6th instar	10	1.01 ± 0.04

calvifrons, and several undescribed species with Caribbean distributions. Secondary sexual characters are highly developed in males of this group. Sex scales are present on the head, thorax, wings, and abdomen of various species. Males of this group are distinguished easily from other *Crocidosema* by the strongly upturned labial palpi and modified scaling on the convex frons, mentioned above.

Larvae of *C. litchivora* will key convincingly to couplet 25 in the "key to some common tortricid larvae on apple, peach and generically related fruits" (Brown 1987: 425). However, they do not fit either couplet of 25, i.e., D1's on A8 are only slightly closer together than D2's, and the pinacula are conspicuous. They can be distinguished from the closely related *C. lantana* by their greater number of crochets: *C. lantana* has 20–30 crochets on prolegs A3–6 and 15–17 on A10 (see MacKay 1959); in contrast, *C. litchivora* has 35–38 on prolegs A3–6 and 20–23 on A10.

Distribution of relatives.—*Crocidosema lantana* was described from Hawaii (Busck 1910) based on specimens imported from Mexico for biological control of weedy lantana (*Lantana camara* L.; Verbenaceae) (Perkins and Swezey 1924, Zimmerman 1978). It subsequently has been introduced into Australia (Tyron 1914, Common 1957) and Micronesia (Zimmerman 1978) for biocontrol. *Crocidosema longipalpana* was described from Puerto Rico (Möschler 1890) and has not been reported from the United States. Material examined of *C. litchivora* indicates that it may be restricted to Central America, Florida, and the Caribbean (including Puerto Rico). It probably is native to southern Florida, southern Texas, Mexico, and the Caribbean. The complex also includes several undescribed species from the Caribbean and Central America.

Based on specimen evidence (IFAS), *C. litchivora* has been in the Homestead area at least since 1992, but in low density. Its increase in abundance in southern Florida since 1992 may be attributable to the increase in acreage of litchi plantings following hurricane Andrew. Owing to the absence of records prior to 1992, it is likely that this Caribbean species is a fairly recent arrival to southern Florida.

Food plants.—In addition to *Litchi chinensis, C. litchivora* has been reared from wampi (*Clausena lansium* (Lour.) Skeels; Rutaceae) (n = 1) and loquat (*Eriobotyra japonica* (Thunb.) Lindl.; Rosaceae) (n = 2) in southern Florida.

Biology

Based on laboratory rearings, the total duration of the immature stages from egg

Table 3. Commercial importation of *Litchi* into the U.S. in 1998.

Country of Origin	# Shipments	Weight
China	17	456,418 kg
Israel	4	16,789 kg
Mexico	83	204,533 kg
Taiwan	14	295,486 kg

Table 4. Tortricidae recorded from *Litchi* worldwide.

Species	Geographic Region	References
Acroclita nigrovenana Kuznetsov	Vietnam, Japan	Nasu 1993
Adoxophyes fasciculana (Walker)	Southeast Asia	Clarke 1976, Diakonoff 1982
Adoxophyes orana (Fischer v. Rosler.)	Hong Kong	Lee & Winney 1981
Archips machoplis (Meyrick)	SE Asia, India	Tuck 1990, Kuroko & Lewvanich 1993
Archips micaceana (Walker)	Thailand	Lee & Winney 1981, Kuroko & Lewvanich 1993
Cnesteboda celligera (Meyrick)	Asia	Diakonoff 1939, 1960, 1982, Kuroko & Lewvanich 1993
Crocidosema lantana Busck	Hawaii	Zimmerman 1978
Crocidosema litchivora	Florida	present paper
Cryptophlebia illepida (Butler)	Hawaii	Zimmerman 1978, Jones 1994
Cryptophlebia ombrodelta (Lower)	Hawaii, Micronesia	Diakonoff 1960, 1968, Clarke 1976, Zimmerman 1978, Jones 1994
Cryptophlebia peltastica (Meyrick)	Micronesia	Clarke 1976, Newton & Crause 1990
Dudua aprobola (Meyrick)	Southeast Asia	Diakonoff 1960, 1982, Clarke 1976
Gymnandrosoma aurantianum (Costa Lima)	Brazil	Costa Lima 1945
Homona coffearia (Nietner)	Asia	Lee & Winney 1981, Kuroko & Lewvanich 1993
Homona eductana (Walker)	Thailand	Kuroko & Lewvanich 1993
Proteoteras implicata Heinrich	Florida	USNM and IFAS specimens
Statherotis leucapis (Meyrick)	Southeast Asia	Clarke 1976, Diakonoff 1982
Statherotis discana (Feld. & Rog.)	Southeast Asia	Nasu, Kawasaki & Arakaki 1993
Thaumatotibia leucotreta (Meyrick)	Africa	Quilici et al. 1988, Newton & Crause 1990

through pupa is 34 ± 1 days. Eggs hatch 3–4 days after oviposition, and there are six larval instars. Duration of all stages is listed in Table 1. Larval head capsule width increases from 0.21 mm in first instars to 1.01 mm in final instars (Table 2). Females begin to oviposit 5 ± 1 days after emergence, with the last oviposition bout coming 15 ± 3 days after emergence. Adults lived 11 ± 7 days. The number of eggs obtained per female (n = 6) was 33 ± 5.

Eggs of *C. litchivora* were found singly or in groups of no more than 3 eggs on a bud. First instars emerge by chewing through the chorion in the region of the micropyle, leaving the empty eggshell in place. At first they feed externally on the bud, but eventually bore into it. Feeding damage is characterized by a small, nearly elliptical hole in the bud, usually accompanied by light brown frass protruding from the hole. First instars feed mostly in buds; later instars bore into young stems, but also feed on flowers, predominantly in the ovary, or bore into developing fruits. When flowers are present, the larvae tie the pollen and petals together with silk and use the inflorescence as a pupation site. If only small fruits are present, larvae chew into the lateral part of the fruit, often leaving it hollow. Once fruits are sufficiently mature, larvae do not attack them; only rarely did we encounter mature fruit with larval feeding damage. Infrequently, larvae leave the bud, inflorescence, or fruit, and roll leaves of the food plant, and pupate in this shelter. At least one species of Tachinidae emerged from late instars (n = 20) collected in the field. Larval feeding can result in significant economic loss as a result of lowered fruit production.

Other Tortricid Pests of Litchi

In 1998, approximately 973,226 kilograms (over 1,000 tons) of litchi were imported into the United States, primarily from China, Taiwan, Mexico, and Israel (Table 3). Imported litchi are treated routinely with methyl bromide to prevent the entry into the United States of exotic pest species (J. Cavey, pers. comm.). However, based on inspections of personal baggage and other cargo, it is likely that hundreds of kilograms of *Litchi* enter this country illegally, undetected, and untreated every year, primarily from the Orient.

The larvae of a large number of Tortricidae have been recorded feeding on litchi in the tropical regions of the world (see Table 4). Although most are reported infrequently, *Cryptophlebia illepida* (Butler), *C. ombrodelta* (Lower), and *C. peltastica* (Meyrick) are major pests of this crop (e.g., Newton and Crause 1990, Jones 1994), particularly in Hawaii and the Far East. Of the 19 species listed in Table 4, three are known from the contiguous United States (i.e., Florida)—*Crocidosema litchivora, C. lantana,* and *Proteoteras implicata* Heinrich. These three appear to be Neotropical, for the most part, ranging into Florida from either Central America or the Caribbean. *Crocidosema litchivora* and *P. implicata* at times have inflicted considerable damage in commercial litchi orchards in Florida, but *C. lantana* apparently has not. The importation of *Litchi* plant stock into Florida from Hawaii creates a potential for the Hawaiian *Litchi* pests, *C. illepida* and *C. ombrodelta,* to inadvertently be brought into Florida. Hence caution must be exercised in the movement of *Litchi* plant material. Because larvae of many of these pests feed primarily in the fruit, the undetected, illegal import of *Litchi* fruit from the Far East creates a much greater potential for the introduction of additional *Litchi* pests from that geographic area.

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FURTHER CHARACTERIZATION OF *PALEOMASTACRIS AMBARINUS* PEREZ ET AL. (ORTHOPTERA: EUMASTACIDAE) FROM DOMINICAN AMBER

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Abstract.—Three new specimens of fossil Eumastacidae in Dominican amber are characterized and identified as the previously described *Paleomastacris ambarinus* Perez et al. 1997. The better preservation of these specimens allows examination of features of the head not visible in the holotype. *Paleomastacris ambarinus* lacks the protruding fastigium typical of extant Hispaniolan Eumastacidae and in this respect seems to resemble Central American Episactinae more closely than those of Hispaniola. This fossil species likely represents an early link between these two extant groups of eumastacids.

Resumen.—Se estudian tres nuevos especímenes de Eumastacidae fósiles en ámbar dominicano y se identifican como el previamente descrito *Paleomastacris ambarinus* Perez et al. 1997. La mejor preservación de estos especímenes permite examinar rasgos de la cabeza no visibles en el holotipo. *Paleomastacris ambarinus* carece del fastigio protuberante típico de los Eumastacidae vivientes en la Hispaniola y en este respecto se asemeja más a los Episactinae centroamericanos que a los de la Hispaniola. Esta especie fósil podría representar una conección temprana entre estos dos grupos vivientes de eumastácidos.

Key Words: amber fossils, Dominican Republic, Eumastacidae, grasshoppers

Fossil eumastacid grasshoppers were known until recently only as compression fossils from North American and Asian locations, varying in age from Miocene (15–30 mya) to lower Jurassic (190 mya) (Zeuner 1944; Sharov 1968; Lewis 1974, 1976; Lin 1980). More recently, Martins-Neto (1991) reported fossil eumastacoids from the lower Cretaceous of the Santana formation in Araripe, Brazil. *Paleomastacris ambarinus* Perez et al. 1997, from the Miocene Dominican amber, is the first eumastacid and only acridomorph grasshopper reported so far from amber. The type specimen (American Museum of Natural History no. DR-10-1795) is a juvenile male with several morphological features that distinguish it from extant Eumastacidae. The extant fauna of eumastacid grasshoppers in Hispaniola comprises at least 5 genera and 10 species (Perez-Gelabert 1999). Although the taxonomic characterization of the group on the island is still incipient, this is probably a nearly complete representation of the lineages found there today. Geologically the amber mines found north of Santiago are considered Miocene in age (15–20 million years old) (Iturralde-Vinent and MacPhee 1996) although others (Lambert et al. 1985) have previously argued that they could be as much as 33–40 million years old, based on studies of nuclear magnetic resonance spectroscopy.

In this paper, I report on three new fossil specimens of Eumastacidae in Dominican amber and assign them to the previously described species *P. ambarinus.* Since these specimens are preserved better than the holotype, I describe features of the head not previously visible and discuss its relationship to extant eumastacids.

SPECIMENS

Through the kind assistance of Robert E. Woodruff and George O. Poinar, Jr., I had the opportunity to examine three eumastacid specimens in Dominican amber. One of these specimens appeared in a photograph together with a hypothetical illustration of its ancient environment in the book "*The Amber Forest*" by Poinar and Poinar (1999).

Specimen MNHNSD (Figs. 4, 6).—Male juvenile, embedded diagonally in an oval-shaped flat piece, approximately 23 × 16 × 6 mm in size and 1.8 grams in weight. The fossil has the dorsal and ventral portions of the head obscured by products of decomposition and detritus. This specimen was donated by Dr. R. E. Woodruff to the entomological collection of the Museo Nacional de Historia Natural, Santo Domingo (MNHNSD).

Specimen O-2-15A (Fig. 5).—Male juvenile, positioned flat and centrally on a golden flattened piece approximately 12 × 6 mm that allows very good visibility of most external features on both sides. Its preservation condition is very good. Deposited in the Poinar collection.

Specimen O-2-15C (Figs. 1, 2, 3).—Male juvenile, included near the top of a 5 mm cubic piece that is polished flat at its base. Also in good preservation condition. Deposited in the Poinar collection.

METHODS

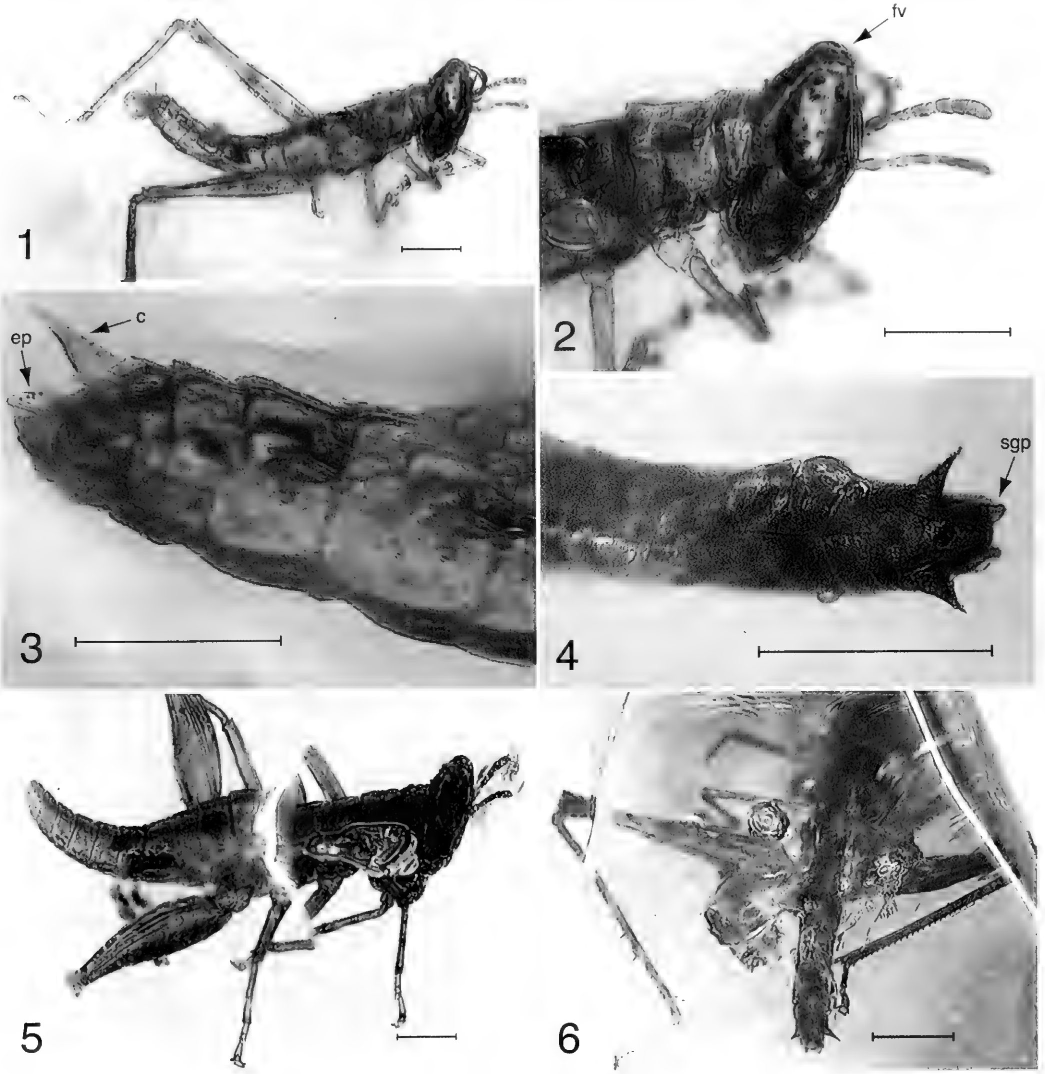
Although measured and studied at different times, the same 7–30× stereoscope fitted with an ocular micrometer with precision to 0.01 mm was used to examine the holotype and the new specimens. The specimens were examined directly without using immersion techniques. Photographs of the included eumastacids were taken with a Sony DKC-5000® digital photo camera mounted on a Leica MZ APO® stereoscope. The fossils were compared to adult and juvenile specimens of several extant Hispaniolan and Central American species.

Paleomastacris ambarinus Perez et al. 1997

Paleomastacris ambarinus Perez et al. 1997: 150 (♂; from Dominican amber; photo of complete specimen, figs. of head, pronotum, legs, hind tibia, abdominal end); Eumastacidae in Poinar and Poinar (1999: 53, photo 49; 57, habitus illustration).

The unique combination of characters that allows the identification of these three new specimens as *P. ambarinus* are the short and flattened pronotum with anterior and posterior margins quadrate; genicular lobe of hind femur forming well-defined spine; triangular epiproct slightly constricted in its middle and elongated just past abdominal end; and cerci simple, slightly globose at base, then finely elongated, slightly projecting at sides of abdominal end. The split male subgenital plate described from the holotype as a unique feature, is somewhat visible in the MNHNSD specimen (Fig. 4), but not in the other two. This is apparently due to the positioning of the specimens in the amber pieces and not to any obscuring debris or imperfection of the matrix.

The approximate dimensions of the new specimens are given in Table 1. As in the holotype, all three specimens represent male juvenile individuals of moderately well-defined morphology. Based on comparisons to nymphs of several extant species, I believe that *P. ambarinus* was probably smaller than all known extant Hispaniolan eumastacids. Both specimens from the Poinar collection show the head intact; the head was incompletely characterized in the original description. In neither specimen



Figs. 1–6. Photos of *Paleomastacris ambarinus*. 1, Specimen O-2-15C. 2, Detail of head in specimen O-2-15C, showing the non-elongated fastigium of vertex (fv). 3, Abdominal end of specimen O-2-15C showing finely pointed cerci (c) and elongated epiproct (ep). 4, Abdominal end of specimen MNHNSD showing split subgenital plate (sgp). 5, Specimen O-2-15A. 6, Specimen MNHNSD. In all figures scale bar represents 0.5 mm.

Table 1. Some approximate dimensions (mm) of the three new specimens of *P. ambarinus* and the previously described holotype.

	Holotype	MNHNSD	O-2-15A	O-2-15C
Body length	5.50	7.10	7.47	6.32
Hind femur length	3.00	4.74	2.89	2.79
Pronotum length	1.00	—	0.74	0.74

does the fastigium of vertex obviously protrude beyond the eyes (Figs. 1, 2, 5). Extant Dominican eumastacids have a distinctively large and protruding fastigium of vertex even as small nymphs. The condition in the amber specimens is rather reminiscent of the Central American Episactinae (*Episactus* Burr, *Gymnotettix* Bruner and *Mayamastax* Uvarov), which also lack this protruding fastigium.

DISCUSSION

Living Hispaniolan eumastacids characteristically occupy defined altitudinal strata of various mountain forests and apparently have rather limited distribution ranges. Because of these characteristics, it is not surprising that the three additional fossil specimens which probably originated in the same area as the type (amber mines of Cordillera Central north of Santiago), represent the described species. The lack of a protruding fastigium in *P. ambarinus* resembles what is found today in extant Central American Episactinae suggesting a closer affinity to them than to extant Hispaniolan species. This interpretation fits models of Caribbean historical biogeography (e.g., Buskirk 1985) that indicate a closer proximity between the Greater Antilles and Central America during the Miocene than today. The phylogenetic relationships within and between the Hispaniolan and Central American Episactinae are not known. The only phylogenetic data available on this group of eumastacids are from the analyses of Rowell and Flook (1998), in which phylogenetic trees based on 12S and 16S mtRNA genes, show the Hispaniolan genera *Antillacris* Rehn & Rehn, *Espagnoleta* Perez-Gelabert and *Espagnolopsis* Perez et al. on one branch of the Episactinae clade somewhat separated from the branch containing the Central American genus *Episactus,* which may be their closest relatives. *Paleomastacris ambarinus* likely represents an early link between these groups that have subsequently evolved, geographically separated from each other for at least 20–30 million years.

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DESCRIPTION OF IMMATURE STAGES OF *TEPHRITIS STIGMATICA* (COQUILLETT) (DIPTERA: TEPHRITIDAE)

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Abstract.—The pre-imaginal stages of *Tephritis stigmatica* (Coquillett) are described. *Tephritis stigmatica* is an oligophagous, multivoltine, facultatively axillary-bud-gall-forming and florivorous tephritid associated with *Senecio* spp. (Asteraceae) in southern California. The egg, first-, second-, and third-instar larvae and puparium are described and figured, and selected characteristics of these stages are compared with those of other southern California *Tephritis.* The egg of *T. stigmatica* is covered by a smooth, membraneous sheath of unknown function. The descriptions of the first, second, and third instars are the most complete reported to date for the genus *Tephritis.* The integumental petals of all three instars are found in medial and lateral positions on the gnathocephalon and increase in numbers from the first to the last instar. The most lateral integumental petal is fused with the stomal sense organ in the first instar. The anterior spiracle has four or five papillae in the second instar, and four papillae in the third instar. The pairs of stelex sensilla surrounding the posterior spiracular plates increase in number from the first to the second instar, and retain the same number and locations, but include two pairs of verruciform sensilla dorsally and laterally in the third instar. The lateral spiracular complexes of the metathorax and first abdominal segment of the second and third instars are described and pictured. The lateral spiracles of the third instar uniquely are prominent on raised peritremes, unlike the second instar, in which they are difficult to locate, as in most other tephritine larvae.

Key Words: Insecta, *Tephritis, Senecio,* Asteraceae, nonfrugivorous Tephritidae, taxonomy of immature stages, egg, larvae, puparium, spiracles

To date, the life histories and immature stages of five species of *Tephritis* have been described in detail from southern California: *T. arizonaensis* Quisenberry (Goeden et al. 1993), *T. baccharis* (Coquillett) (Goeden and Headrick 1991), *T. joanae* Goeden (Goeden 1993, 2001b), *T. teerinki* Goeden (Goeden 2001c) and *T. footei* Goeden (Goeden 2002). The immature stages of a sixth species, *T. stigmatica* (Coquillett), are described in this paper to facilitate their comparison with the immature stages of the other five species. The biology of *T. stigmatica* is relatively well known (Tauber and Toschi 1965; Goeden 1988, 1993).

Materials and Methods

Monthly samples of overwintered, axillary bud galls containing eggs, larvae, puparia of *T. stigmatica* were collected in February, March and April, 2000, from *Senecio flaccidus* Lessing var. *douglassii* (deCandolle) B. Turner and T. Barkley at the same two southern California sites used in my 1984–85 field study of the life history of this tephritid (Goeden 1988): (1)

south of Lamont Peak at Spanish Needle Creek; Sequoia National Forest (north section); (T)ownship 22 (S)outh, R(ange) 36 E(ast); Kern County; and (2) 2 km south of Pearblossom; T5 N(orth), R10 W(est); Los Angeles County. Samples of galls were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, description, photography, and measurement. Three eggs, 18 first-, 16 second-, and 17 third-instar larvae, and three puparia dissected from galls were preserved in 70% EtOH for scanning electron microscopy (SEM). Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Central Facility for Advanced Microscopy and Microanalysis, University of California, Riverside.

Plant names used in this paper follow Hickman (1993); tephritid names follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c, d), Goeden et al. (1993), Goeden and Headrick (1991), Goeden and Teerink (1999), Teerink and Goeden (1999), and our earlier works cited therein. Voucher specimens of immature stages of *T. stigmatica* reside in my research collection. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 6.

RESULTS AND DISCUSSION

Immature stages.—The egg, first-, second-, and third-instar larvae, and puparium of *Tephritis stigmatica* are described below.

Egg: Four eggs measured *in situ* in field-collected, immature, overwintered galls were white, opaque, smooth, elongate-ellipsoidal, 0.8 mm long by 0.2 mm wide, smoothly rounded at tapered basal end (Fig. 1A); pedicel button-like, 0.02 mm long, circumscribed apically by different-sized, irregularly-, semi-rectangular, or semicircular-shaped aeropyles arranged singly or in

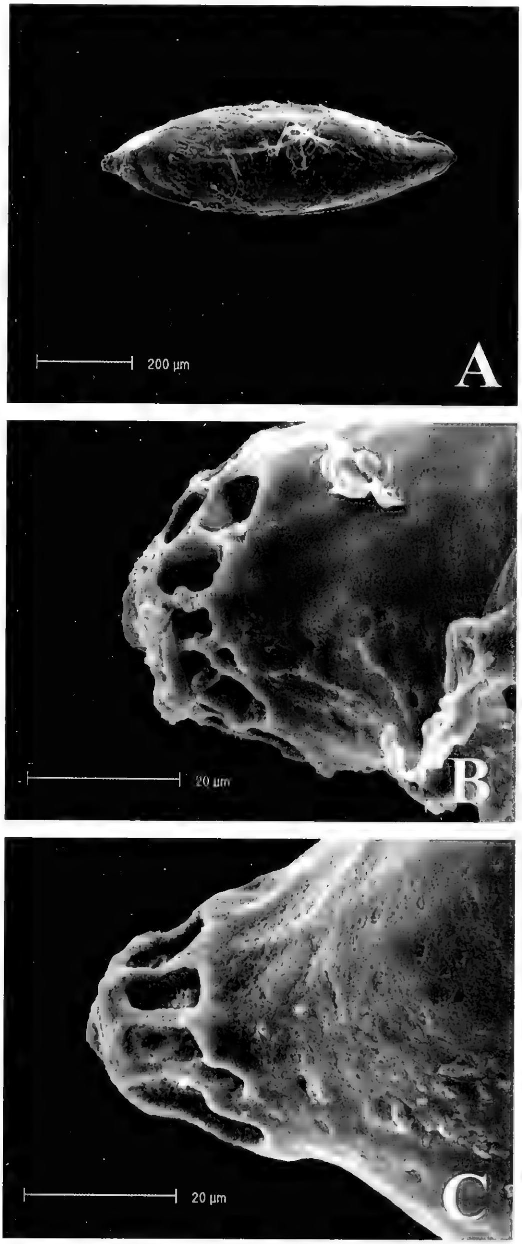

Fig. 1. Egg of *Tephritis stigmatica*: (A) habitus, anterior to left; (B) pedicel showing pattern and shapes of aeropyles; (C) pedicel of a different egg, for comparison.

rows of two parallel to the long axis of the egg (Figs. 1B, C).

The egg of *T. stigmatica* (Fig. 1A), like those of *T. joanae* (Goeden 2001b), *T. teerinki* (Goeden 2001c), and *T. footei* (Goeden 2002) differs from eggs of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993) by lacking prominent polygonal reticulation of the chorion. Also, the egg of *T. stigmatica*, like those of *T. teerinki, T. joanae,* and *T. footei,* apparently is covered by a smooth, membraneous sheath (Figs. 1A, B; Goeden 2001b, c, 2002), which remains intact and is not partly shed and peeled back during oviposition as in *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). The function of this membraneous sheath remains unknown. It was first reported for *T. arizonaensis* by Goeden et al. (1993), who then belatedly recognized it in *T. baccharis,* and apparently only has been reported to date from the eggs of these six species of *Tephritis.* In *T. arizonaensis* (Goeden et al. 1993), this membraneous sheath also is prominently, longitudinally striated. Weak longitudinal striations are present at the anterior, pedicellar end of the egg of *T. footei,* but otherwise are not seen on the rest of the egg body (Goeden 2002).

First instar larva: White, cylindrical (Fig. 2A); gnathocephalon conical; dorsal sensory organ well-defined, domed (Fig. 2B-1); anterior sensory lobe (Fig. 2B-2) with terminal sensory organ (Fig. 2B-3), lateral sensory organ (Fig. 2B-4), supralateral sensory organ (Fig. 2B-5), and pit sensory organ (Fig. 2B-6); stomal sense organ (Figs. 2B-7, C-1) ventrolaterad of anterior sensory lobe and fused with flattened, protrudent, lateral integumental petal (Figs. 2B-8, C-2) dorsad of each mouthhook (Figs. 2B-9, C-3), two medial integumental petals between anterior sensory lobes, upper one bulbous, and lower one, less prominent (Fig. 2B-10); mouthhook (Figs. 2B-9, C-3) bidentate; median oral lobe laterally compressed, apically rounded, ventrally flattened (Figs. 2B-11, C-4), basally attached to labial lobe (Fig. 2B-12) bearing two, prominent apical pores; posterior spiracular plate bears two ovoid rimae (Fig. 2D-1), ca. 0.01 mm long, and four interspiracular processes (Fig. 2D-2), each with one or two, foliose branches with one to three, apical teeth, longest branch measuring 0.01 mm; stelex sensillum dorsolaterad (Fig 2E) of posterior spiracular plate, ventrolateral stelex sensillum not seen; intermediate sensory complexes (Figs. 2D-3, F) each with a stelex sensillum (Fig. 2F-1) and a medusoid sensillum (Fig. 2F-2).

Among southern California *Tephritis* spp., the first instar previously was described in detail only for *T. teerinki* (Goeden 2001c), which along with the partial description for the first instar of *T. footei* (Goeden 2002), provide at least some basis for comparison. For example, the integumental petal fused with the stomal sense organ in *T. stigmatica* (Figs. 2B-7, 8, C-1, 2) also distinguishes the first instars of *T. teerinki* (Goeden 2001c) and *T. footei* (Goeden 2002), as well as the first instars of at least five species of *Neaspilota* (Goeden 2001a), from subsequent instars. This character was first reported for the first instar of *Trupanea vicina* (Wulp) (Goeden and Teerink 1999). The integumental petals of the first instars of *T. footei* (Goeden 2002) and *T. stigmatica* (Figs. 2B-8, 10, C-2) are similarly shaped and separable into lateral and medial positions. The mouthhooks of the first instars of *Tephritis teerinki* (Goeden 2001c) and *T. stigmatica* (Figs. 2B-9, C-3) are bidentate. The intermediate sensory complexes ventral to the posterior spiracular plates of the first instars of *T. footei* (Goeden 2002) and *T. stigmatica* (Figs. 2D-3, F) are similarly composed of a stelex sensillum and a medusoid sensillum, and the posterior spiracular plates are flanked, at least dorsolaterally in both species, by stelex sensilla (Goeden 2002, Fig. 2E)

Second instar larva: White, cylindrical, rounded anteriorly, truncated posteriorly, body segments well-defined (Fig. 3A); gnathocephalon conical, anteriorly flat-

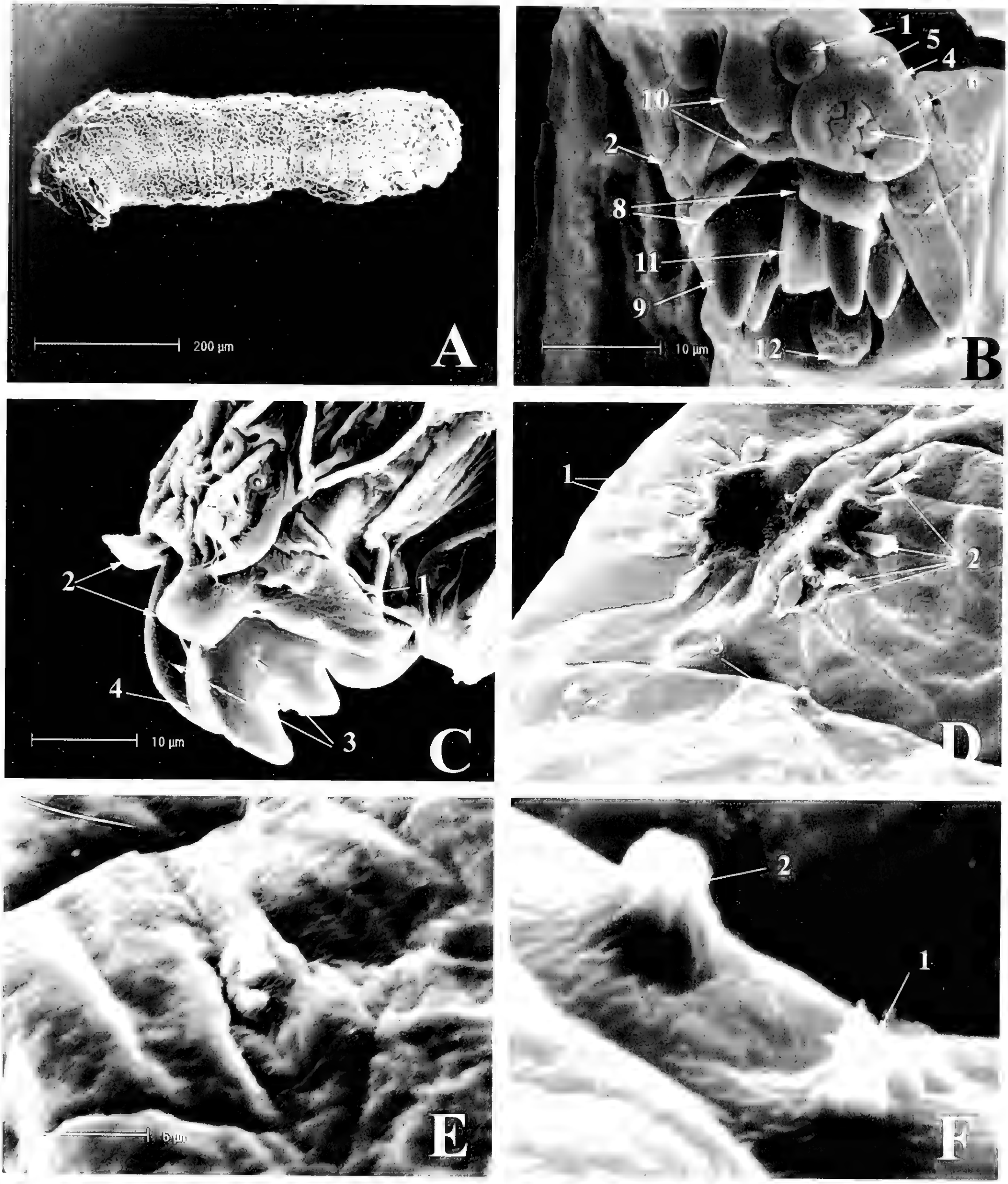

Fig. 2. First instar of *Tephritis stigmatica*: (A) habitus, anterior to left; (B) gnathocephalon, ventrofrontal view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—stomal sense organ, 8—lateral integumental petal, 9—mouthhook, 10—median integumental petal, 11—median oral lobe, 12—labial lobe; (C) gnathocephalon, dorsolateral view, 1—stomal sense organ, 2—lateral integumental petals, 3—mouthhooks, 4—median oral lobe; (D) caudal segment, 1—rimae, 2—interspiracular processes, 3—intermediate sensory complexes; (E) dorsolateral stelex sensillum; (F) intermediate sensory complex, (1) stelex sensillum and (2) medusoid sensilllum.

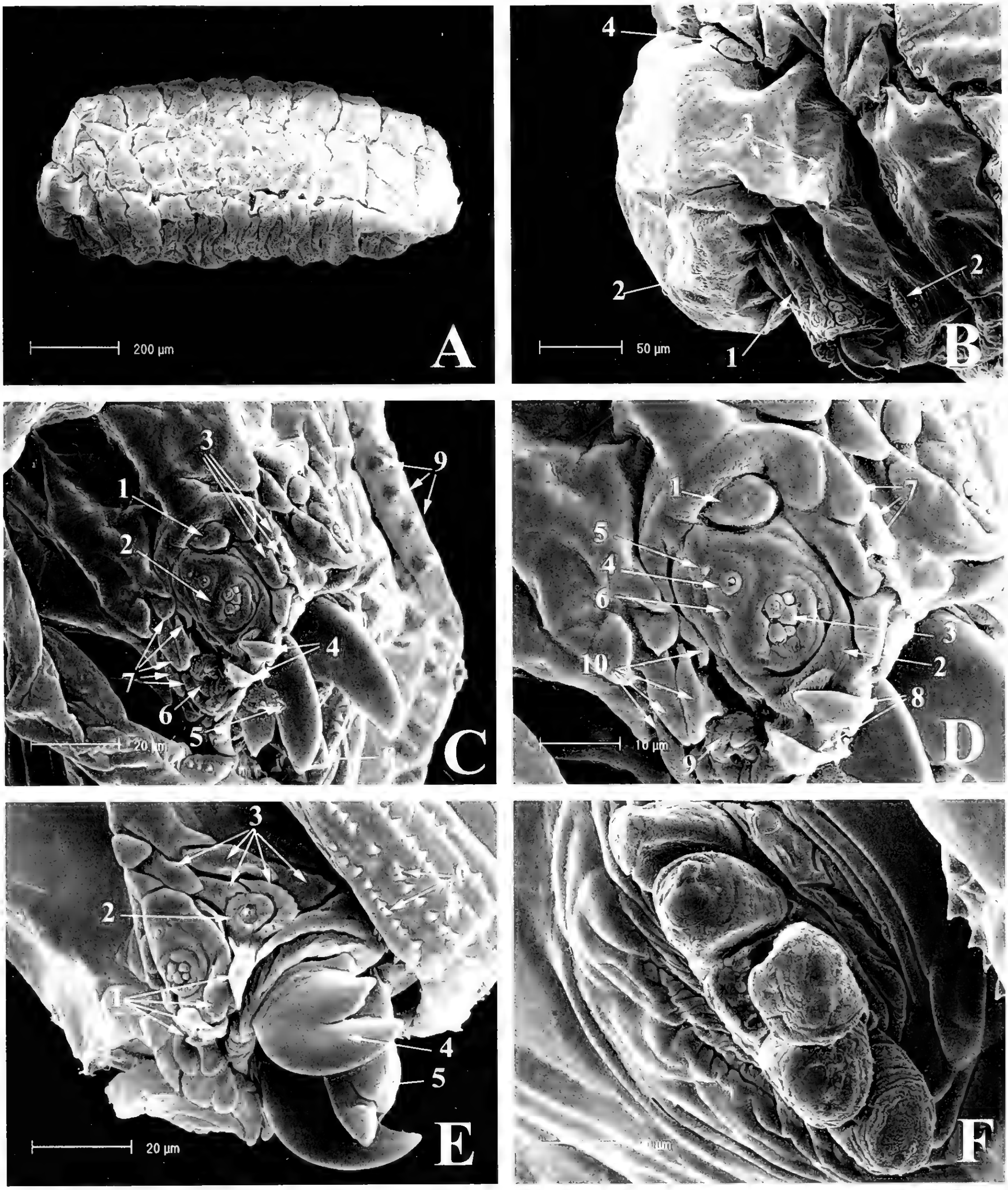

Fig. 3. Second instar of *Tephritis stigmatica*: (A) habitus, anterior to left; (B) prothorax, lateral view, 1—median vertical suture on gnathocephalon, 2—minute acanthae, 3—verruciform sensilla, 4—anterior spiracle; (C) gnathocephalon, dorsolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—medial integumental petals, 4—lateral integumental petals, 5—mouthhook, 6—stomal sense organ, 7—oral ridges, 8—median oral lobe, 9—minute acanthae; (D) close-up of gnathocephalon, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—medial integumental petals, 8—lateral integumental petals, 9—stomal sense organ, 10—oral ridges; (E) gnathocephalon, ventrolateral view, 1—lateral integumental petals, 2—stomal sense organ, 3—oral ridges, 4—mouthhook, 5—median oral lobe, 6—minute acanthae; (F) anterior spiracle with middle papilla partially displaced.

tened, and medially cleaved by a vertical suture (Fig. 3B-1); posteriorly directed, spinose, minute acanthae incompletely circumscribe gnathocephalon anteriorly (Figs. 3B-2, C-9, E-6), minute acanthae also circumscribe meso- and metathorax, and abdominal segments A1–A2 anteriorly, with bands of minute acanthae widening ventrally and laterally on A3–A5, but narrowing again on A6–A8, prothorax also circumscribed dorso- and lateromedially by verruciform sensilla (Fig. 3B-3); dorsal sensory organ well-defined, rounded dome (Figs. 3C-1, D-1); anterior sensory lobe (Figs. 3C-2, D-2) bears terminal sensory organ (Fig. 3D-3), lateral sensory organ (Fig. 3D-4), supralateral sensory organ (Fig. 3D-5), and pit sensory organ (Fig. 3D-6); three or four, medial, integumental petals in vertical row between anterior sensory lobes to each side of medial crease (Figs. 3C-3, D-7) and two each, lateral, spatulate or papillate, integumental petals (Figs. 3C-4, D-8, E-1) in two rows above each mouthhook (Fig. 3C-5), and separate from stomal sense organ (Figs. 3C-6, D-9, E-2) ventrolaterad of anterior sensory lobe; four or five, complete oral ridges (Figs. 3C-7, D-10, E-3) laterad of each anterior sensory lobe; mouthhook tridentate (Figs. 3C-5, E-4); median oral lobe laterally compressed, apically pointed (Figs. 3C-8, E-5); anterior spiracle with total of four (Fig. 3B-4) or five (Fig. 4A-1), doliform or subquadrate papillae; lateral spiracular complexes of metathorax (Fig. 4A) and first abdominal segment (A1) (Fig. 4C) each consist of a spiracle (Figs. 4A-2, B, C-1, D) and two, verruciform sensilla (Figs. 4A-3, C-2), one sensillum vertical to the other; posterior spiracular plate (Figs. 4E-1, F) bears three ovoid rimae (Fig. 4F-1), ca. 0.02 mm long, and four interspiracular processes (Fig. 4F-2), each with two to four foliose branches, each with one or two apical teeth, longest branch measuring 0.01 mm; stelex sensilla dorsad (Fig. 4E-2), dorsolaterad (Fig. 4E-3), laterad (Fig. 4E-4), and ventrolaterad (Fig. 4E-5) of posterior spiracular plate; intermediate sensory complexes (Figs. 4E-6, F-3) each with a stelex sensillum and a medusoid sensillum.

The habitus of the second instar of *T. stigmatica* (Fig. 3A) approximates those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), *T. joanae* (Goeden 2001b), *T. teerinki* (Goeden 2001c), and *T. footei* (Goeden 2002). The anterior spiracle of the second instar of *T. stigmatica* bears four (Fig. 3B-4) or five (Fig. 4A-1), doliform or subquadrate papillae, not five subquadrate or subglobose papillae like those of *T. joanae* (Goeden 2001b) and *T. footei* (Goeden 2002), nor four, doliform papillae like *T. teerinki* (Goeden 2001c). The lateral spiracular complexes of the meso- and metathorax (Fig. 4A) and A1 (Fig. 4C) are the first described to date for a second instar *Tephritis*. Likewise, the position and number of stelex sensilla surrounding the posterior spiracular plate are recorded here for the first time for a second instar *Tephritis*. Noteworthy, too, is the pair of dorsal stelex sensilla (Fig. 4E-2), not reported in any other tephritine second instar. These dorsal sensilla also are present in the third instar of *T. stigmatica* (see below, Fig. 7A), in which they are verruciform, not stelex sensilla. Only minor differences in the number of branches on the interspiracular processes, i.e., one to two for *T. footei* (Goeden 2002), one to three for *T. teerinki* (Goeden 2001c), versus two to four for *T. stigmatica* (Fig. 4F-2) and *T. joanae* (Goeden 2001b), were noted. Also, the branches of the interspiracular processes of *T. stigmatica* are foliose (Fig. 4F-2), like those of the second instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), not lanceolate, like those of *T. footei* (Goeden 2002).

Third instar larva: White, ellipsoidal, distinctly segmented, tapered anteriorly, truncated posteriorly (Fig. 5A); gnathocephalon conical, anteriorly flattened, and medially cleaved by a vertical suture (Fig. 5B-1); posteriorly directed, spinose, minute acanthae sparse on dorsal margin and ventral margin of gnathocephalon (Figs. 5B-2,

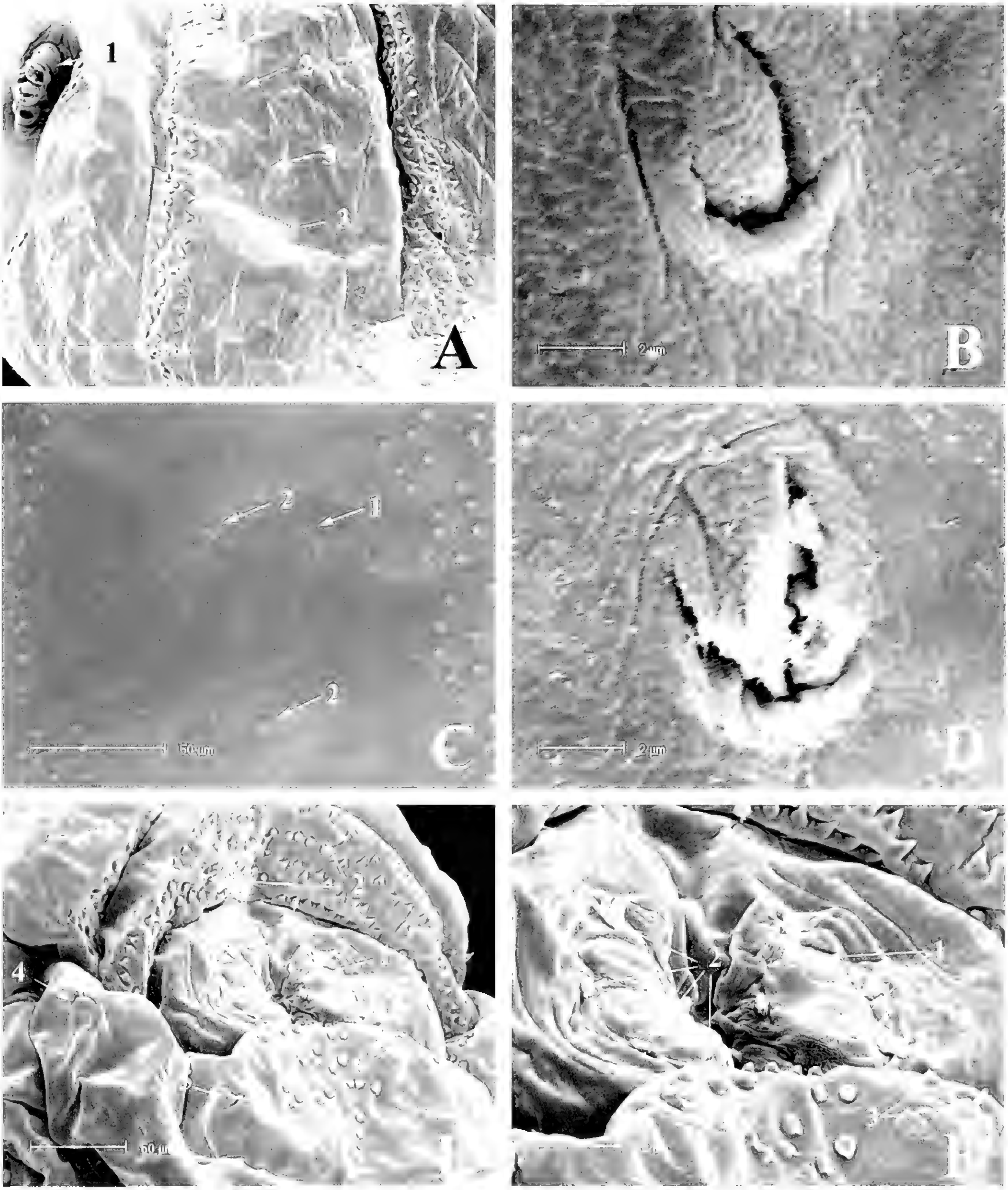

Fig. 4. Second instar of *Tephritis stigmatica*, continued: (A) lateral spiracular complex of metathorax, 1—anterior spiracle, 2—metathoracic lateral spiracle, 3—verruciform sensilla; (B) metathoracic lateral spiracle; (C) lateral spiracular complex of first abdominal segment, anterior to right, 1—spiracle, 2—verruciform sensilla; (D) lateral spiracle on first abdominal segment; (E) caudal segment, 1—posterior spiracular plate, 2—dorsal stelex sensilla, 3—dorsolateral stelex sensillum, 4—lateral stelex sensillum, 5—ventrolateral stelex sensilla, 6—intermediate sensory complex; (F) posterior spiracular plate, 1—rimae, 2—interspiracular processes, 3—intermediate complexes.

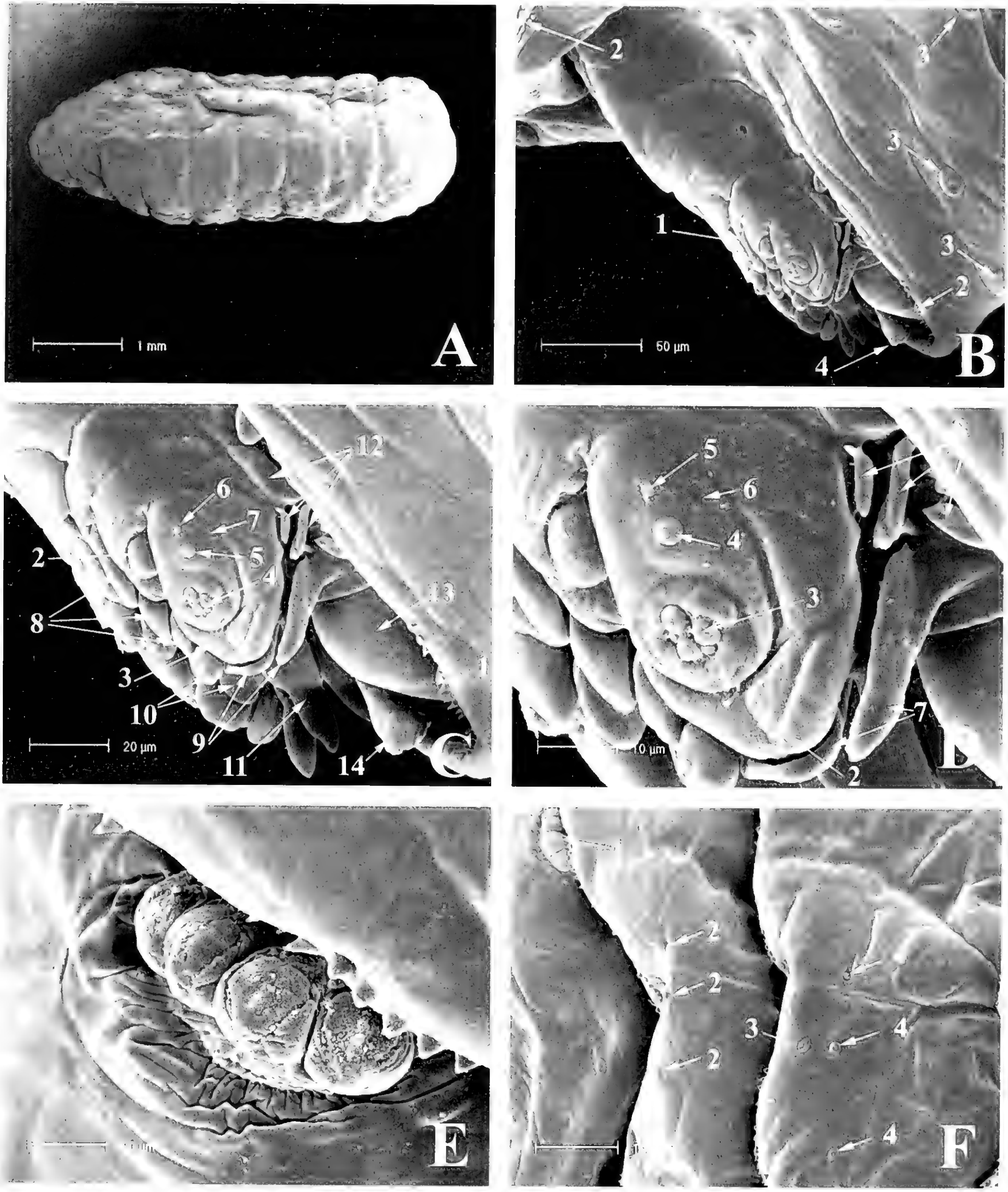

Fig. 5. Third instar of *Tephritis stigmatica*: (A) habitus, anterior to left; (B) gnathocephalon, frontolateral view, 1—vertical, medial suture of gnathocephalon, 2—minute acanthae, 3—verruciform sensilla, 4—median oral lobe; (C) gnathocephalon, frontolateral view, 1—minute acanthae, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—terminal sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ, 7—pit sensory organ, 8—medial integumental petals, 9—lateral, spatulate, integumental petals, 10—lateral, papillate, integumental petals, 11—central, papilliate, integumental petal, 12—oral ridges, 13—mouthhook, 14—median oral lobe; (D) 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—lateral, spatulate, integumental petals, 8—oral ridges; (E) anterior spiracle; (F) mesothoracic and metathoracic, lateral spiracular complexes, 1—anterior spiracle, 2—verruciform sensilla on mesothorax, 3—metathoracic spiracle, 4—verruciform sensilla on metathorax.

C-1) and in bands that circumscribe intersegmental areas of thorax and abdomen, bands widest ventrally and laterally between segments A3 and A6; verruciform sensilla circumscribe the prothorax medially (Fig. 5B-3); dorsal sensory organ well-defined, domed (Figs. 5C-2, D-1); anterior sensory lobe (Figs. 5C-3, D-2) bears terminal sensory organ (Figs. 5C-4, D-3), lateral sensory organ (Figs. 5C-5, D-4), supralateral sensory organ (Figs. 5C-6, D-5), and pit sensory organ (Figs. 5C-7, D-6); three or four, medial integumental petals (Fig. 5C-8) and two, lateral, spatulate (Figs. 5C-9, D-7) and two, lateral, papillate, integumental petals (Fig. 5C-10) in two rows of two above each mouthhook, plus a central pair of papillate petals (Fig. 5–11), the lower, lateral, spatulate petal (Fig. 5C-9) separate from stomal sense organ (present, but not shown), ventrolaterad of anterior sensory lobe; at least three complete oral ridges (Figs. 5C-12, D-8) laterad of each anterior sensory lobe; mouthhook (Fig. 5C-13) at least bidentate; median oral lobe (Figs. 5B-4, C-14) laterally compressed, apically pointed; anterior thoracic spiracle (Figs. 5E, F-1) on posterior margin of prothorax bears four subglobose or subquadrate papillae; mesothoracic, lateral spiracular complexes with three verruciform sensilla (Fig. 5F-2) in vertical row, mesothoracic spiracle not seen; metathoracic lateral spiracular complex with well-defined spiracle, on an oval, raised peritreme (Figs. 5F-3, 6A-1, B-1, C) and three verruciform sensilla (Figs. 5F-4, 6A-2) in vertical series posterior of spiracle; lateral spiracular complex of first abdominal segment (A1) (Fig. 6D) with well-defined spiracle on a circular, raised peritreme (Figs. 6A-3, D-1, E-1, F) anteriorad of two verruciform sensilla (Fig. 6E-2), one vertical to the other; caudal segment (Fig. 7A) bears posterior spiracular plates (Figs. 7A-1; B) surrounded by pair of dorsal verruciform sensilla (Figs. 7A-2, C), pair of dorsolateral stelex sensilla (Figs. 7A-3, D), pair of lateral verruciform sensilla (Figs. 7A-4, E), and ventrolateral pair of stelex sensilla (Fig. 7A-5); each posterior spiracular plate bears three ovoid rimae (Fig. 7B-1), ca. 0.06 mm in length, and four, five to six-branched, single-, bi-, or trifurcately-tipped, interspiracular processes, the longest ca. 0.03 mm long (Fig. 7B-2); intermediate sensory complex (Fig. 7A-6, F) with a stelex sensillum (Fig. 7F-1) and a medusoid sensillum (Fig. 7F-2).

The habitus of the third instar of *T. stigmatica* differs from those of four other described congeners in at least two ways. The ellipsoidal shape of the third instar (Fig. 5A) is closest to the elongate-ellipsoidal shape of the third instar of *T. footei* (Goeden 2002), both of which appear intermediate to the ovoidal shape of the third instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c) and the cylindrical shape ascribed to third instars of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). The prothorax (Fig. 5B) is much smoother than that of *T. footei* (Goeden 2002), that uniquely is circumscribed by many integumental petals, and thus, is much more like the prothoracic segments of the four other species of *Tephritis* examined to date (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c). Few minute acanthae anteriorly circumscribe the prothorax of the third instars of *T. stigmatica* (Figs. 5B-2, C-1) like that of *T. footei* (Goeden 2002), rather than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c). On the other hand, the gnathocephalon, or at least the anterior sensory lobes of all six species are separated by a vertical medial suture (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c, 2002).

The integumental petals in the third instars of all six congeners examined to date are arranged in a double row above each mouthhook, but those of *T. stigmatica* (Figs. 5C-9, 10) occur in two rows of two like *T. teerinki* (Goeden 2001c) and *T. footei* (Goeden 2002), with an additional, me-

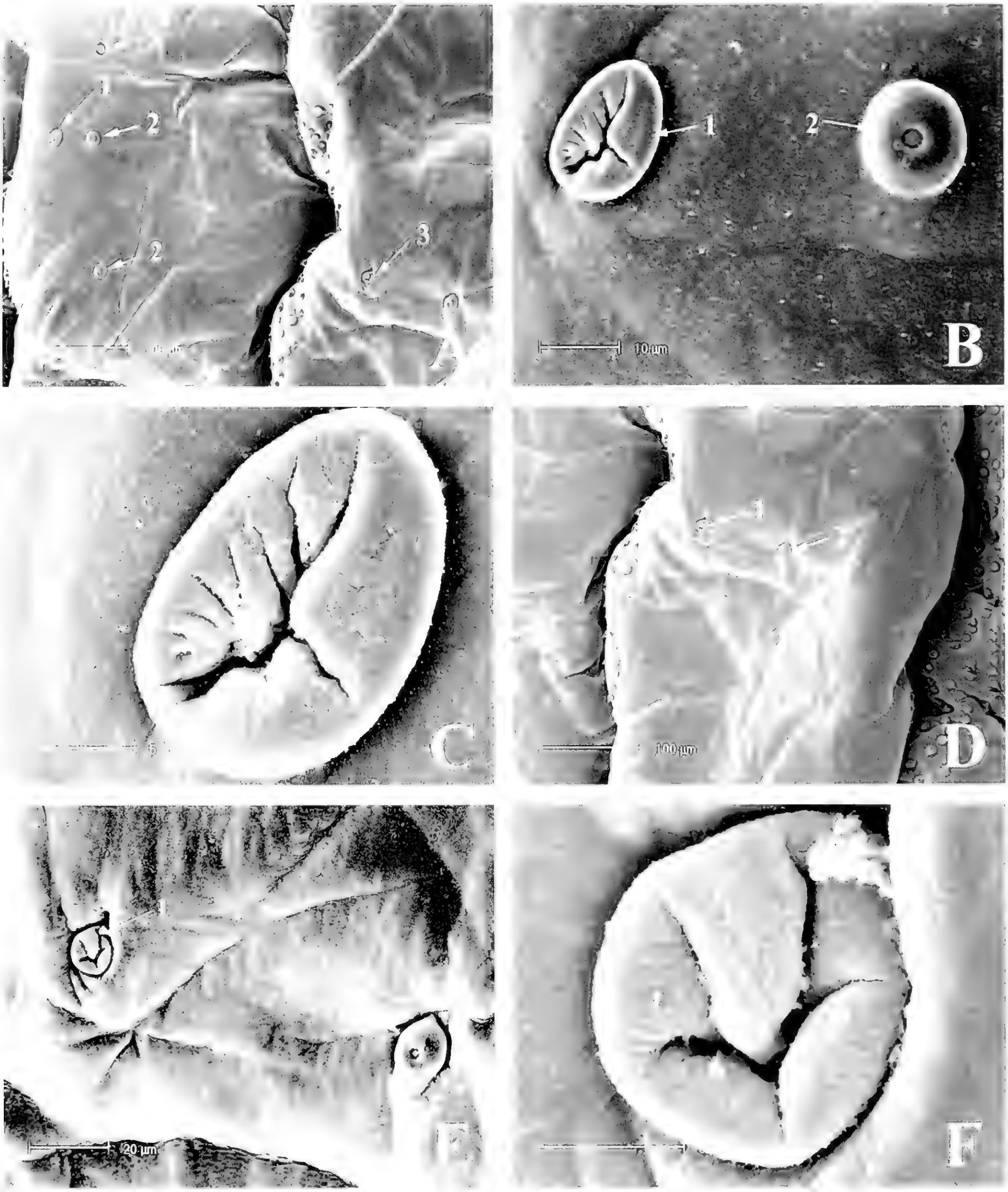

Fig. 6. Third instar of *Tephritis stigmatica*, continued: (A) lateral spiracular complex of metathorax, 1—metathoracic, lateral spiracle, 2—verruciform sensilla, 3—lateral spiracle on A1; (B) 1—metathoracic, lateral spiracle, 2—verruciform sensillum; (C) metathoracic, lateral spiracle; (D) lateral spiracular complex of first abdominal segement, 1—lateral spiracle on A1, 2—verruciform sensilla; (E) 1—lateral spiracle on A1, 2—verruciform sensillum; (F) lateral spiracle on A1.

dial pair papillate in shape (Fig. 5C-11). However, the integumental petals of *T. teerinki* (Goeden 2001c), *T. footei* (Goeden 2002), and *T. stigmatica* (Fig. 5C-8) are still fewer in number than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b). Only *T. footei* and

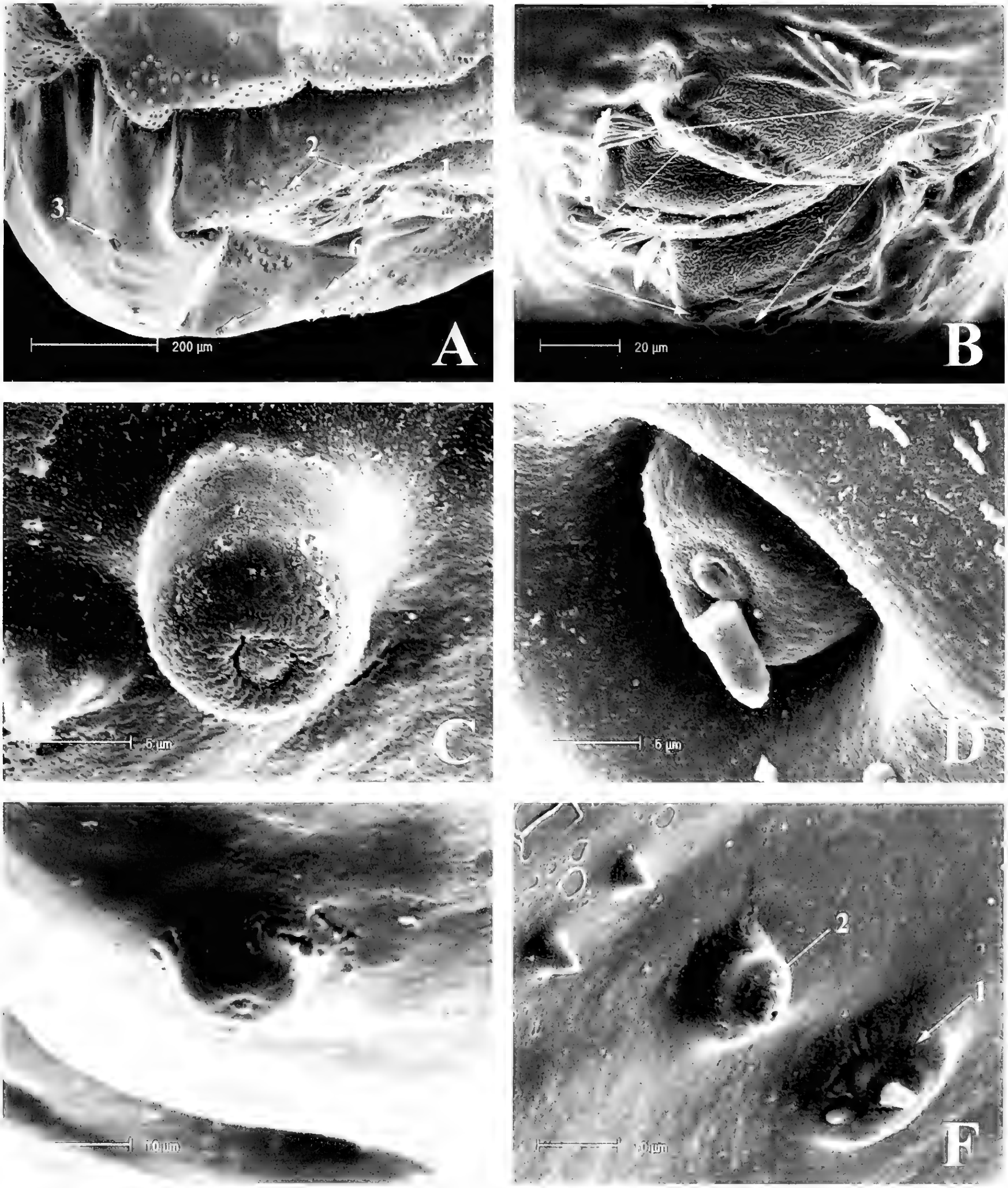

Fig. 7. Third instar of *Tephritis stigmatica*, continued: (A) caudal segment, 1—posterior spiracular plate, 2—dorsal, verruciform sensilla, 3—dorsolateral, stelex sensillum, 4—lateral, verruciform sensillum, 5—dorsoventral, stelex sensillum, 6—intermediate sensory complexes; (B) posterior spiracular plate, 1—rimae, 2—interspiracular processes; (C) dorsal, verruciform sensillum; (D) broken, dorsolateral, stelex sensillum; (E) lateral, verruciform sensillum; (F) intermediate sensory complex, 1—stelex sensillum, 2—medusoid sensillum.

T. teerinki apparently lack the additional, medial, integumental petals found in a vertical double row above these lateral papillae, one to each side of the medial depression separating the anterior sensory lobes (Fig. 5C-8; Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c, 2002). The integumental petals increase in

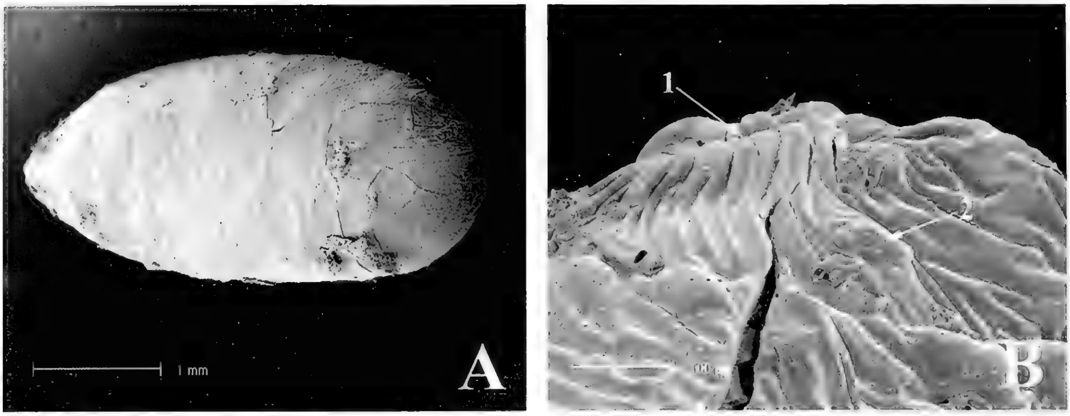

Fig. 8. Puparium of *Tephritis stigmatica*: (A) habitus, anterior to left, (B) anterior end, 1—invagination scar, 2—anterior spiracle.

number between the last two instars of *T. footei* (Goeden 2002), *T. joanae* (Goeden 2001b), *T. teerinki* (Goeden 2001c), and *T. stigmatica* (Figs. 3C-3, 4, D-7, 8, E-1; 5C-8, 9, 10, 11).

The anterior spiracle of the third instar of *T. stigmatica* (Figs. 5E, F-1) bore four papillae, instead of four or five papillae in the second instar (Figs. 3B-4, 4A-1). In comparison, the anterior spiracle of *T. footei* (Goeden 2002) bears three or four papillae in the third instar, and one or two less than the second instar; whereas, *T. joanae* (Goeden 2001b) has three papillae in the second instar, and three or four in the third instar; and *T. teerinki* (Goeden 2001c) has four in the second instar and five in the third instar.

The lateral spiracular complexes on the mesothorax, metathorax, and A1 of third instar *T. stigmatica* (Figs. 5F, 6A, D) are the most fully described among the six species of *Tephritis* reported to date. The lateral spiracles on the metathorax and A1 are uniquely prominent in the third instar occurring as they do on raised peritremes (Figs. 6B-1, C, D-1, F), and thus, are not difficult to locate as they are in the second instar (Figs. 4B, D), and in most other Tephritinae larvae examined by my coworkers and me to date.

Goeden (2001c) discussed the sensilla surrounding the posterior spiracular plates of the third instars that apparently differ in number and kinds among the *Tephritis* species examined to date. These sensilla are unique in *T. stigmatica,* which alone has a pair of dorsal verruciform sensilla (Fig. 7A-2) and a pair of lateral stelex sensilla (Figs 7A-4, D) in addition to dorsolateral and ventrolateral pairs of verruciform sensilla, like those that surround the caudal segments of the third instars of *T. footei* (Goeden 2002), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c). In addition, each of these four species bears a ventral pair of intermediate spiracular complexes (Fig. 7A-6, F), each composed of a stelex sensillum (Fig. 7F-1) and a medusoid sensillum (Fig. 7F-2), which bears short apical papillae typical of this type of chemosensillum (Goeden 2001a, b, c, d; Goeden and Teerink 1999, and references therein). Thus, two pairs of dorsal sensilla surrounding the spiracular plate of the third instar are verruciform (Fig. 7A-2), not all stelex sensilla, as in the second instar (Fig. 4E-2).

Puparia: Dull black, ovoidal, and smoothly rounded at both ends (Fig. 8A); the anterior end bears the invagination scar (Fig. 8B-1) and anterior spiracles (Fig. 8B-2). Twenty-one puparia averaged 4.22 ± 0.06 (range, 3.65–4.6) mm in length; 1.93 ± 0.025 (range, 1.75–2.15) mm in width.

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THE STATUS OF SOME PLESIOMORPHIC BLISSID BUGS (HETEROPTERA: LYGAEOIDEA: BLISSIDAE) FROM THE ORIENT

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Abstract.—Five species of Oriental Blissidae are removed from the genus *Ischnodemus* and placed in the genus *Capodemus*. **New combinations** are *Capodemus ambiguus* (Slater, Ashlock, and Wilcox 1969), *C. fumidus* (Slater, Ashlock, and Wilcox 1969), *C. nigrocephalus* (Slater, Ashlock, and Wilcox 1969), *C. sinuatus* (Slater, Ashlock, and Wilcox 1969), and *C. thoracicus* (Distant 1909). ***Capodemus nepalensis,* n. sp.**, is described from Nepal. A discussion of the zoogeographic and phylogenetic relationships is included as are two dorsal view illustrations.

Key Words: Blissidae, Lygaeoidea, Oriental, Ethiopian, Gondwanaland, plesiomorphic

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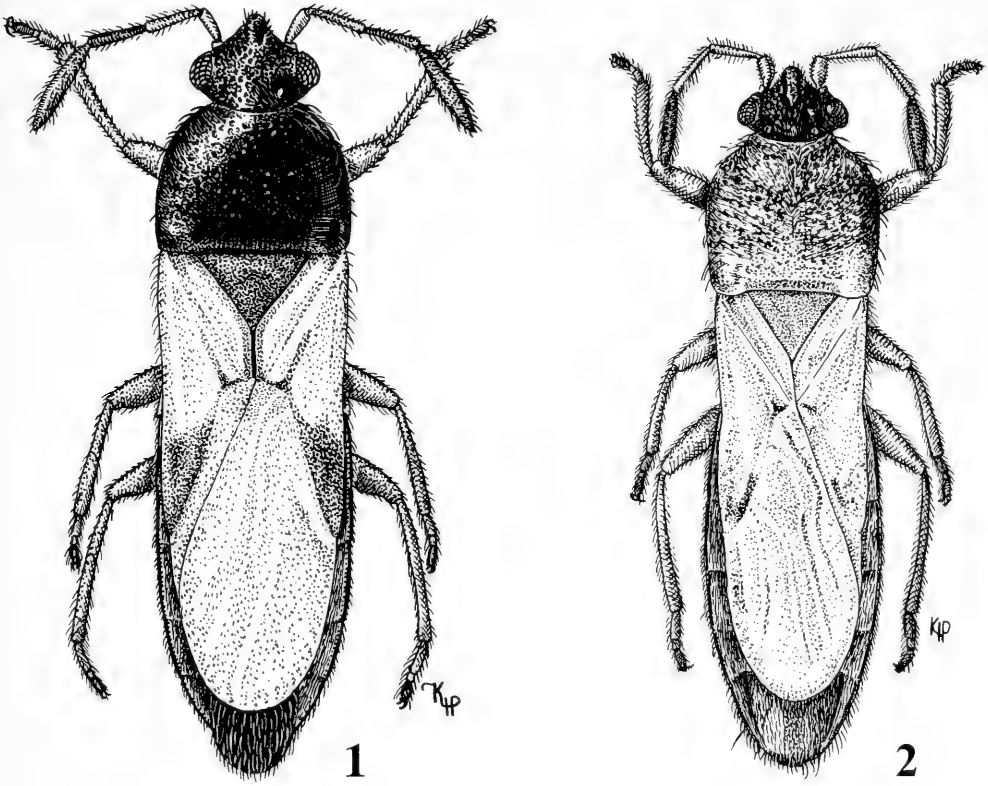
For many years I have been perplexed by the relationships of a group of species found in the Orient. As early as 1969 in a joint paper, the late P. D. Ashlock, D. Wilcox and I described several species from Thailand and "Indo-China" and placed them in the genus *Ischnodemus*. We emphasized that they were not closely related to other species of that genus and were placed there more for convenience until relationships could be better understood to avoid creating another generic entity.

The chief problem presented by these species was that the condition of the fore coxal cavities, which Slater (1979) used extensively in his phylogenetic analyses, appears to break down among what otherwise seems to be a closely related group of species. Slater and Ashlock (1976) had previously discussed this coxal cavity feature and pointed out that it was not correlated with body length, but that several conditions existed (see Slater 1979 for a discussion). The primary differentiating character was whether the fore coxal cavities were open (as they are in most lygaeoids) or closed as they are in many blissid genera.

In the tiny Oriental species considered here and at present placed in *Ischnodemus* Fieber [*ambiguus* Slater, Ashlock, and Wilcox (Fig. 1); *fumidus* Slater, Ashlock, and Wilcox; *nigrocephalus* Slater, Ashlock, and Wilcox (Fig. 2); *sinuatus* Slater, Ashlock, and Wilcox and *thoracicus* (Distant)], the coxal cavities are open in *ambiguus* and *fumidus* but very narrowly closed in the other species. All of these species have the dorsal surface of the head and pronotum completely shining and non-pruinose (considered to be an apomorphic condition), the scutellum completely pruinose as is the entire propleuron up to a line just below the lateral edge of the pronotum, and all have rounded metathoracic scent gland auricles. These species were retained in *Ischnodemus* by Slater (1979) but with a footnote that at least *ambiguus* and *fumidus* did not belong belong there and might be more closely related to the South African genus *Capodemus* Slater and Sweet.

In the 1980's, the late Thomas Woodward sent me a series of remarkable micropterous blissids from Mt. Gingera, ACT,



Figs. 1–2. 1, *Capodemus ambiguus*, dorsal view. 2, *C. nigrocephalus*, dorsal view.

Australia. These specimens resembled *Capodemus* species in many ways, differing chiefly in having a completely pruinose dorsal body surface and especially a paramere with a unique outer projection, which is greatly enlarged and curves across the base of the blade (see Slater 1986). Since the pruinose body is considered plesiomorphic in the blissids (Slater 1979), I described these specimens as representing a new genus, *Archaedemus* (Slater 1986), but noted close resemblance in many ways to *Capodemus* Slater and Sweet. In the same paper I described an additional genus (*Propinquedemus*), based on a micropterous female from the mountains of Burma that I had held for many years hoping for additional specimens, especially a male and/or a macropter. This female was also noted as being similar to species of *Capodemus,* but like *Archaedemus* also had a completely pruinose dorsal surface of the pronotum and scutellum, but that the head was shining and non-pruinose, except at the extreme base.

This paper is an attempt to place the five Oriental species listed above relative to *Capodemus, Archaedemus,* and *Propinquedemus.* I also describe an additional species of *Capodemus* from Nepal.

Capodemus is represented in South Africa by a number of species. There is a marked radiation in the extreme southwestern Cape and the genus is not known in Africa other than from South Africa and Zimbabwe. The fore coxal cavities are narrowly open. Very importantly in members of this genus the pruinosity differs from species to species. The propleuron may be completely pruinose (*variabilis* Slater and Sweet and a number of other species), or confined to the pleural area anterior to the acetabulum. The dorsal surface of the head and pronotum are mostly shining and non-pruinose but pruinosity is frequently present along the lateral area of the dorsal surface of the pronotum. Scutellar pruinosity is present, but the meson is always shining and the pruinosity is either confined to the anterior half of the scutellum or to the lateral areas. The parameres are simple and bladelike without any enlargement or twisting of the outer lobe. Spines may be present or absent on the fore femur. See Slater and Sweet (1972) for an extended discussion of variability among the South African species.

All of the Oriental species mentioned above, plus an additional undescribed species, fall within the defining characters of *Capodemus,* except those with very narrowly closed fore coxal cavities. These species thus should be removed from *Ischnodemus* and placed in *Capodemus.*

Such action has interesting zoogeographic implications. It suggests that *Capodemus* as here defined is an old taxon probably of Gondwana origin. This conclusion is based upon the close relationship to *Archaedemus* in Australia and the essential absence of *Ischnodemus* in the otherwise rich Oriental blissid fauna. In the Orient these small *Capodemus* species seem to be rare and largely replaced by such genera as *Macropes, Cavelerius, Dimorphopterus, Iphicrates,* and a number of bizarre highly modified and specialized taxa. The presence of these Oriental *Capodemus* gives the impression of a taxon largely supplanted by other taxa. By contrast *Ischnodemus* is abundant and diverse in Africa with many species showing close relationship to Neotropical species. It is also noteworthy that African species of *Capodemus* are largely confined to the extreme southwestern Cape, known to be the refuge area for many otherwise replaced taxa. Such a distribution suggests an old taxon, once more widely distributed in Africa but supplanted by other taxa and now confined largely to refugial cool areas of winter rainfall in the southwestern Cape Province.

A distribution such as that of *Ischnodemus,* with strong Neotropical-Ethiopian relationships and only marginal Old World Tropical relationships (i.e., essential absence from the Oriental Region), is not common in the Lygaeoidea and suggests not only the antiquity of the *Capodemus* fauna, but also the radiation of *Ischnodemus* after the separation of western Gondwanaland.

The following new combinations are thus established:

Capodemus ambiguus (Slater, Ashlock, and Wilcox 1969), **new combination** from *Ischnodemus.*

Capodemus fumidus (Slater, Ashlock, and Wilcox 1969), **new combination** from *Ischnodemus.*

Capodemus nigrocephalus (Slater, Ashlock, and Wilcox 1969), **new combination** from *Ischnodemus.*

Capodemus sinuatus (Slater, Ashlock, and Wilcox 1969), **new combination** from *Ischnodemus.*

Capodemus thoracicus (Distant 1909), **new combination** from *Ischnodemus.*

All measurements are in millimeters.

KEY TO ORIENTAL SPECIES OF *CAPODEMUS*

1. Fore femur with a bifid spine present . . *sinuatus*
–′ Fore femur mutic 2
2. Prosternal pruinosity confined to area anterior to coxae . . . . *thoracicus*
–′ Entire prosternum pruinose 3
3. Scutellum shining distally on meson . . *nepalensis*
–′ Entire scutellum pruinose 4
4. Head black, strongly contrasting with pale color of pronotum and rest of body (Fig. 2) . . . . *nigrocephalus*
–′ Head nearly unicolorous with dorsal surface of pronotum 5
5. Membrane of forewing (except veins) completely white or hyaline; second antennal segment pale testaceous (Fig. 1) . . . . *ambiguus*
–′ Membrane of forewing smoky brown with differing white veins; second antennal segment dark brown to black . . . . *fumidus*

Capodemus fumidus (Slater, Ashlock, and Wilcox)

This species was described from Thailand. I have examined three males and one female from SABAH: Tomani, 1.IX.1983 (G. F. Hevel & E. Steiner) (National Museum of Natural History and J. A. Slater collections). These specimens appear to be conspecific with *fumidus* but have the second antennal segment pale.

Capodemus nepalensis Slater, new species

Description.—Head, anterior two-thirds of pronotum, scutellum, pleuron and sternum black. A conspicuous sub-apical corial macula (not reaching lateral corial margin) and a small trianguloid macula at distal end of radial vein near anterior end of apical corial margin and distal half of fourth antennal segment dark brown. Posterior one-third of pronotum and lateral margins of abdominal sterna dark yellowish tan. Legs and antennal segments pale yellow. Clavus, corium and membrane white, latter with veins slightly infuscated. Head and pronotum dorsally and median area distally on scutellum shining, non-pruinose, remainder of scutellum pruinose. Lateral surface of head and thorax (dorsally to lateral pronotal margin) entirely pruinose. A pair of large ovoid black spots on mesosternum. Metathoracic scent gland dull reddish. Dorsal surface bearing numerous semi-decumbent silvery hairs.

Head non-declivent, eyes not stalked but set well away from anterior pronotal margin. Length head 0.46, width 0.60, interocular space 0.36. Lateral pronotal margins little narrowed from humeral angles to level of calli, then strongly curving mesad to anterior margin. Length pronotum 0.62, width 0.90. Length scutellum 0.31, width 0.42. Length claval commissure 0.32. Metathoracic scent gland auricle broadly rounded, ovoid. Fore femur moderately incrassate, mutic. Antenna slender, filiform. Length antennal segments I 0.12, II 0.31, III 0.31, IV 0.42. Labium relatively short, barely reaching anterior area of mesosternum, latter with a distinct median furrow. Length labial segments I 0.22, II 0.28, III 0.16, IV 0.22. Total body length 2.92.

Type material.—Holotype: ♂ NEPAL: Meglavly Terai. Chitwan Nat. Park 7.IV.86 H. Brailovsky. In National Museum of Natural History, Smithsonian Institution, Washington, DC. Paratypes: 2 ♂, same data as holotype. In Instituto de Biologia, Universidad Nacional Autonoma de Mexico and J. A. Slater collections.

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ADDITIONS TO *PHYLLOPHAGA* SUBGENUS *CHLAENOBIA* (COLEOPTERA: MELOLONTHIDAE: MELOLONTHINAE) FROM GUATEMALA

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Abstract.—Three new species of *Phyllophaga* (*Chlaenobia*) are described from eight Guatemalan localities: ***P. fraternaria*** from cloud forests and coffee plantations at 1,320–1,800 m in the departments of San Marcos and Quetzaltenango; ***P. schusteriana*** from pine-oak forests at 1,500 m in the departments of Alta and Baja Verapaz; and ***P. marilucasana*** from oak forests at 1,600–2,100 m in the departments of Santa Rosa, Sacatepequez, and Sololá. Drawings of male genital capsules, female genital plates, metatibiae, and tarsal claws are provided. *Phyllophaga* (*Chlaenobia*) *aegrota* (Bates) and *P.* (*C.*) *scabripyga* (Bates) are reported for the first time in Guatemala.

Resúmen.—Se describen tres especies nuevas de *Phyllophaga* (*Chlaenobia*) representadas por 34 ejemplares procedentes de ocho localidades guatemaltecas: ***P. fraternaria*** de un bosque nebular y plantaciones de cafeto situados entre 1,320 y 1,800 m en los departamentos de San Marcos y Quetzaltenango; ***P. schusteriana*** de bosques de pino-encino situados a 1,500 m en los departamentos de Alta y Baja Verapaz, y ***P. marilucasana*** de bosques de encinos ubicados entre 1,600–2,100 m en los departamentos de Santa Rosa, Sacatepequez y Sololá. Se incluyen ilustraciones de las cápsulas genitales masculinas, de las placas genitales femeninas, de las metatibias y de las uñas tarsales. También se registran por primera vez para Guatemala a *P.* (*Chlaenobia*) *aegrota* (Bates) and *P.* (*C.*) *scabripyga* (Bates).

Key Words: *Phyllophaga,* May beetles, new species, montane forests, Guatemala

Species of the *Phyllophaga* subgenus *Chlaenobia* have the following combination of characters: body elongate, slender; dorsal tegument shiny, yellowish, glabrous; head without transverse carina on the vertex; mesotibiae with one complete oblique carina at the middle of external surface; tarsomeres depressed, elongate, usually with abundant setae on ventral side; tarsal claws bifid o narrowly bifurcated; sexual dimorphism usually noticeable in the form and surface of the pygidium, shape and lenght of tibial spurs and width of tarsomeres. At present, the subgenus consists of 18 species distributed between Texas and Panama (Chapin 1935; Morón 1986, 1992).

Blackwelder (1944) listed only *Phyllophaga* (*Chlaenobia*) *rodriguezi* (Bates) and *P.* (*C.*) *tumulosa* (Bates) from Guatemala. Field work between 1994–1997 led to the discovery of *P.* (*C.*) *aequata chiapensis* (Chapin), *P.* (*C.*) *latipes* (Bates), *P.* (*C.*) *vexata* (Horn), and two undescribed species of this subgenus in Guatemala (Cano and

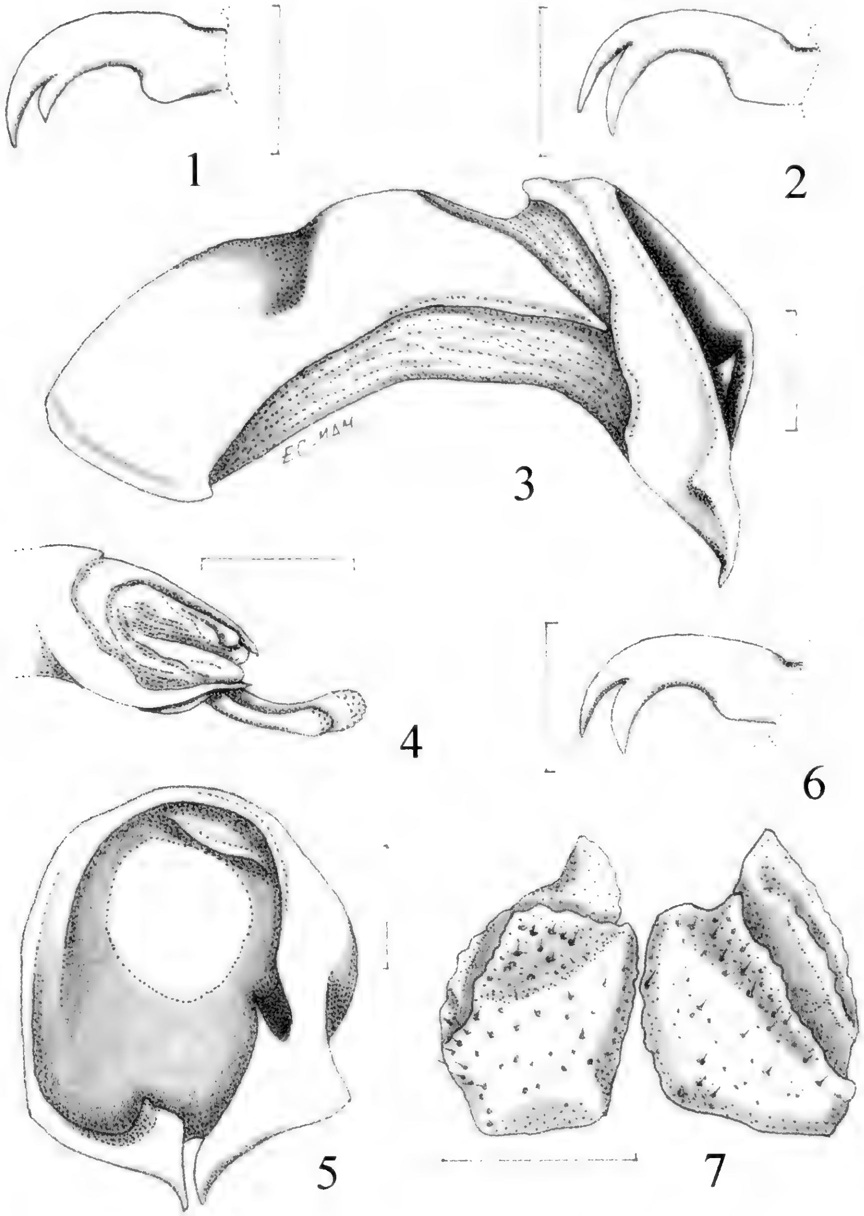
Morón 1998). Recently, E. Cano and J. Monzón obtained samples of two species not known from Guatemala, another undescribed species from departments of Alta Verapaz and Santa Rosa, and many new locality records of all the other species except *P.* (*C.*) *rodriguezi,* confirming that the subgenus is represented in Guatemala by at least ten species. Geographic distribution of six of these species range between southern United States, Mexico, Guatemala and Costa Rica, but the other four appear to be restricted to the Guatemalan mountains. In support of current studies of *Phyllophaga* (*Chlaenobia*) by M. A. Morón, we describe three additional species from Guatemala. Two new country records are also presented.

The terms used in the descriptions are those of Morón (1986, 1992). Drawings were made with the aid of a camera lucida and stereomicroscope; measurements were obtained with an ocular micrometer or caliper. Acronyms used in the text are as follows: UVGC = Universidad del Valle de Guatemala; UNSM = University of Nebraska State Museum, Lincoln; and MXAL = private collection, M. A. Morón, Xalapa, México.

Phyllophaga (*Chlaenobia*) *fraternaria* Cano and Morón, new species

(Figs. 1–7)

Description.—*Holotype male*: Clypeus yellowish brown, disk reddish brown, anterior border darker, frons reddish brown, vertex darker; pronotum shiny yellowish, borders reddish; elytra straw yellowish without macroscopic vestiture, glabrous; mouthparts, sterna, pygidium and legs shiny straw yellowish. Clypeus 2.94× wider than long, anterior border sinuate, with elevated margin, surface glabrous, slightly irregular, almost plain, with many uniformly distributed, deep, rugose punctures. Frontoclypeal suture sinuate and deeply impressed. Frons 1.92× wider than long, glabrous, convex to plain, regularly and deeply, rugo-punctate. Vertex without punctures. Antenna 10-segmented, with 3-segmented club, lamellae narrower than length of basal segments combined (0.86:1). Frons 2.94× wider than dorsal diameter of each eye. Eye canthus long and narrow, with 7–8 setae. Labrum bilobed, deeply sinuate, with scattered long, slender setae on borders. Mentum slightly concave, impunctate, with scarce lateral setae, anterior border sinuate. Pronotum 1.74× wider than long and 2.35× wider than frons. Pronotal disk shiny, with round, moderately deep punctures separated by less of one diameter, forming rugo-punctate texture; lateral borders widely angulated, lateral marginal bead with scattered, short or long, slender setae; basal bead strongly indicated, except in front of scutellum where it is indicated only by scarce punctures; anterior angles obtuse, not prominent; posterior angles not directed downward, obtuse. Scutellum 1.45× wider than long, with some minute punctures. Elytron 2.65× longer than wide, shiny, glabrous, densely rugo-punctate; punctures small, slightly deep, separated by 1–2 diameters; epipleural border very wide at base, narrow along complete margin, with some scattered, short, slender setae; humeral callus rounded, prominent; apical callus rounded. Metathoracic wings completely developed. Propygidium shiny, yellowish with scattered, transversal punctuation and many short decumbent setae towards basal border. Pygidium convex, shiny, strongly rugose, but without visible punctures, with rounded-conical prominence located toward middle of preapical border, basal border without setae; apical margin with 7 long, slender setae; basal margin complete. Pterosternum with moderately dense, long yellowish setae. Visible abdominal sternites II to IV of similar length, slightly concave, with scattered, minute setae at middle; sternite V with wide transverse concavity, almost plain toward midline, with 2 procumbent, short setae near middle; posterior border with marginal bead clearly impressed. Anal plate short, slightly concave at midline, posterior bor-



Figs. 1–7. *Phyllophaga* (*Chlaenobia*) *fraternaria*. 1, Male protarsal claw, lateral view. 2, Male metatarsal claw, lateral view. 3, Genital capsule, lateral view. 4, Apex of aedeagus, dorsolateral view. 5, Parameres, distal view. 6, Female protarsal claw, lateral view. 7, Female genital plates, ventral view. Scale lines = 1 mm, except figs. 1, 2, 6 = 0.5 mm.

der thickened, poorly crenulate at sides of midline, with 10 long and short erect setae along complete border. Protibia shorter than protarsus (0.56:1), with external border tridentate, proximal tooth much shortened, preapical spur narrow, nearly straight, apex acute, half as long as 2nd protarsomere. Mesotibia with one oblique, sharp, setiferous carina on external side; upper apical spur straight, narrow, and 1.33× longer than lower spur. Metatibia shorter than metatarsus (0.63:1), with one oblique, sharp, setiferous carina on external side; upper apical spur articulated, curved, apex acute, slightly shorter than basal metatarsomere, and 1.45× longer than lower spur; lower apical spur articulated with tibial border, with acute apex. Tarsomeres depressed, elongate, with enlarged apices, with some setae apically and two lines of long, thick setae on flattened ventral side. Protarsal claws narrowly cleft, with lower tooth shorter than upper tooth; meso- and metatarsal claws with lower tooth slightly shorter than upper tooth (Figs. 1–2). Genital capsule with large parameres, dorsally and ventrally fused, asymmetrical, apex of each elongated, acute, tooth-like and directed downward. Aedeagus with two internal projections, one of them notably largest, and apex directed upward (Figs. 3–5). Tectum (= phallobase) shortened, with dorsal depression near middle. Length of genital capsule from apex of parameres to border of basal piece: 5.4 mm. Total body length: 17.0 mm. Humeral width: 7.3 mm.

Allotype female: Similar to male except as follows: clypeus, frons and pronotum reddish brown; head with more fine punctures; antenna with lamellae of segments 8–10 slightly shorter or equal to the length of six preceeding segments combined. Visible abdominal sternites II to V convex, with setiferous punctures near middle; anal plate convex, with 3 scattered setiferous punctures, and 10 slender setae at posterior border. Pygidium very convex, without conical prominence, with 10 setae along apical border. Protibia with teeth of external border wider and longer than in male. Both apical spurs of metatibia articulated, wide, lanceolate and curved. Protarsus longer than protibia (1.17:1). Tarsal claws similar on all legs; lower tooth slightly shorter than upper (Fig. 6). Ventral genital plates moderately sclerotized, symmetrical, with scattered short setae, with shallow depression near apex, apical and lateral borders markedly serrate; dorsal genital plates with borders markedly serrate, setae on distal border (Fig. 7). Total body length: 19.0 mm. Humeral width: 7.7 mm.

Variation.—*Male:* Similar to holotype except as follows: Head and pronotum reddish brown or yellowish brown; some specimens with reddish punctures on pronotum; mentum punctate and micropunctate or only densely micropuntate; pygidium with preapical process less, equal or more prominent, with more or less apical setae; abdominal sternites II–IV with more or less setae, sternite V with not so wide transverse concavity or without concavity, almost plain. Total body length: 17.2–18.0 mm; humeral width: 7.0–7.9 mm. *Female:* similar to allotype except head and pronotum yellowish brown, disc and apical border of anal plate with more or less setae, lower tooth of tarsal claws almost equal or slightly shorter than upper. Total body length: 17.2–18.2 mm; humeral width: 7.0–7.9 mm.

Type material.—Described from 13 ♂, 6 ♀. Holotype ♂ UVGC: Guatemala: San Marcos, La Fraternidad, 1,800 m, 5/10-II-1994, bosque nuboso, J. Monzón". Allotype ♀ UVGC: Guatemala: Quetzaltenango, Viejo Palmar, Fca. San Juan Patzulín, 1,320 m, 21-III-1998, I. Chavez. Paratypes: same data as holotype (1♂) (MXAL); same data except 6-III-1994 (2♂) (UVGC); except 25/29-III-1994, 1850 m (1♂, 2♀) (MXAL); except 15/17 IV 1994 (7♂, 3♀) (UVGC); Guatemala: San Marcos, El Tumbador, Fca. Australia, 1,510 m, 4-IV-1998, J. Amau (1♂) (UVGC).

Type locality.—La Fraternidad, department of San Marcos, Guatemala (aprox. 14°55′N; 91°50′W).

Biological data.—Males and females of *P. fraternaria* were collected at UV and Hg lights in median altitude cloud forests and coffee plantations, at 1,320–1,950 m altitude. Phenology: February (2), March (6), April (11).

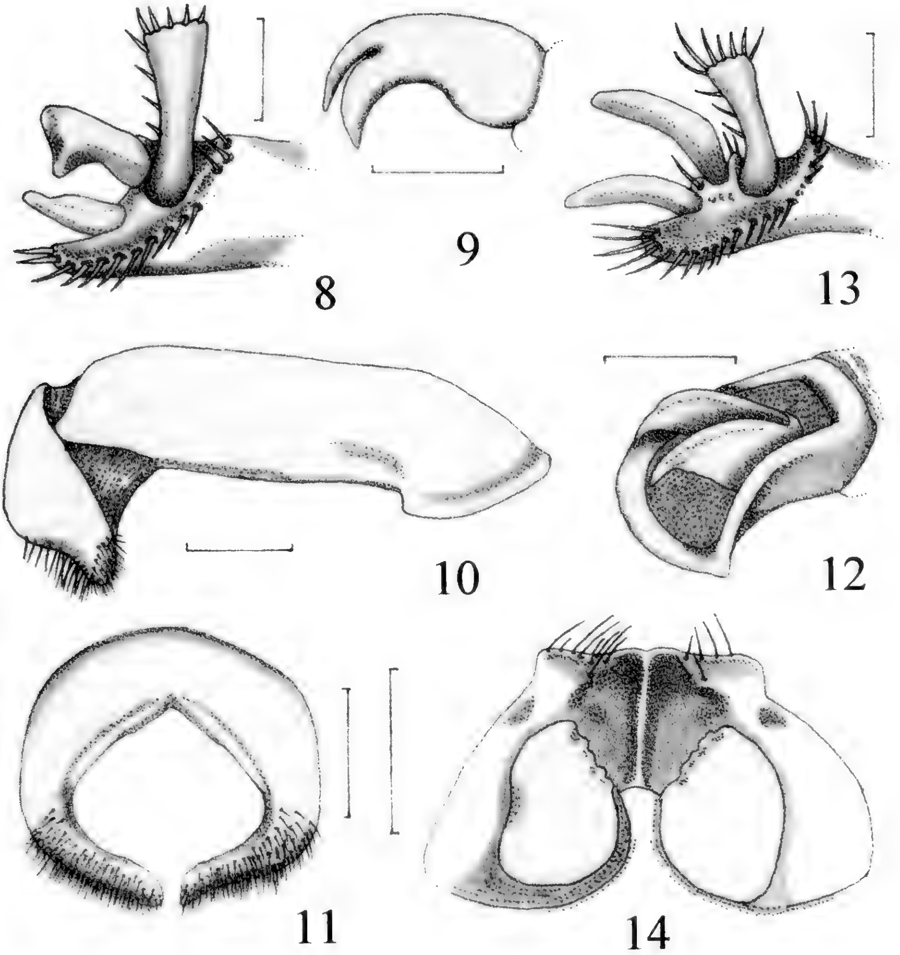
Remarks.—*Phyllophaga* (*Chlaenobia*) *fraternaria* belong to the species group "*vexata*" (*sensu* Morón 1986). By body shape, size, color, general vestiture, punctuation on the clypeus, pronotum and elytra, as well as the general shape of the male genital capsule, it is similar to *P.* (*Chirodines*) *zunilensis* (Bates), *P.* (*Chlaenobia*) *solanophaga* Morón, and *P.* (*Chlaenobia*) *ratcliffeiana* Morón. However the detailed structure and proportions of the parameres and aedeagus are clearly different in all of those species. Also, the narrowly cleft hind tarsal claws separate *P. fraternaria* from *P. zunilensis* and the coarsely rugose pigydium and its preapical prominence separate it from *P. solanophaga* and *P. ratcliffeiana.*

Etymology.—The species name is derived from the type locality, La Fraternidad, a town near the Mexican border.

Phyllophaga (*Chlaenobia*) *schusteriana* Cano and Morón, new species

(Figs. 8–14)

Description.—*Holotype male:* Clypeus reddish brown, disk reddish brown, anterior border darker, frons and vertex reddish brown; pronotum shiny straw yellowish, borders reddish; elytra straw yellowish; mouthparts reddish brown, sterna, pygidium and legs shiny straw yellowish. Clypeus 3.04× wider than long, anterior border sinuate, with elevated margin, surface with microscopic vestiture, slightly convex, with many uniformly distributed, close, deep, almost circular, rugose punctures. Frontoclypeal suture sinuate and deeply impressed. Frons 2.09× wider than long, convex, regularly and deeply, rugo-punctate. Vertex with few small punctures. Antenna 10-segmented, with long 3-segmented club, lamellae slightly short or equal to length of basal segments combined (0.99:1). Frons 3.61× wider than dorsal diameter of each eye, with microscopic vestiture. Eye canthus long and narrow, with 12–13 setae. Labrum bilobed, deeply sinuate, with scattered long, slender setae on borders. Mentum concave, impunctate, with scarce lateral setae, anterior border sinuate. Pronotum 1.94× wider than long and 2.4× wider than frons. Pronotal disk shiny, with microscopic vestiture and round, slightly deep, rugose punctures regularly separated by 1–2 diameters, more dense and rugose toward lateral borders; lateral borders widely angulated, lateral marginal bead slightly crenulate, with scattered, short or long, slender setae; basal bead complete, strongly indicated; anterior angles obtuse, not prominent; posterior angles not directed downward, obtuse. Scutellum 1.37× wider than long, with some minute punctures. Elytron 2.82× longer than wide, shiny, with microscopic vestiture, densely rugo-punctate; punctures small and shallow, separated by 1–2 diameters; 2nd elytral stria prominent, well marked along it complete length, except at basis; epipleural border very wide at base, narrow along complete margin, with some scattered, long, slender setae; humeral callus rounded, prominent; apical callus rounded. Metathoracic wings completely developed. Propygidium shiny, yellowish with scattered, minute punctuation and minute decumbent and procumbent setae. Pygidium triangular, convex, shiny, rugo-punctate, with shallow punctures regularly distributed, separated by 1–2 diameters, basal border without setae; apical margin almost straight with 16 long, slender setae, preceeding by transverse depression transversely micro-rugose; basal margin effaced medially. Pterosternum with moderately dense, long yellowish setae. Visible abdominal sternites II to V of similar length, very concave, with microscopic setae in middle and a few more long setae intermixed, more abundant on sternite II; posterior border with marginal bead clearly impressed. Anal plate long, slightly concave, posterior border thickened, notched at midline, with a few long, erect setae along complete border. Protibia shorter than protarsus (0.49:1), with external border tridentate, proximal tooth well marked but much shortened, preapical spur narrow, straight, apex acute, half as long as 2nd protarsomere. Mesotibia with one oblique, sharp, setiferous carina on external side; upper apical spur straight, narrow, and 1.2× longer than lower spur. Metatibia equal to the



Figs. 8–14. *Phyllophaga* (*Chlaenobia*) *schusteriana*. 8, Apex of male metatibia, latero-distal view. 9, Male protarsal claw, lateral view. 10, Genital capsule, lateral view. 11, Parameres, distal view. 12, Apex of aedeagus, dorsolateral view. 13, Apex of female metatibia, laterodistal view. 14, Female genital plates, ventral view. Scale lines = 1 mm, except fig. 9 = 0.5 mm.

length of metatarsus, without carina on external side, laterally flattened on ventral half and clearly widened toward the apex (Fig. 8); upper apical spur articulated, very curved, apex truncated and wide, slightly shorter than basal metatarsomere, and 1.14× longer than lower spur; lower apical spur articulated with tibial border, with basal ⅔ wide and apical ⅓ narrowed with apex truncated. Tarsomeres depressed, elongate, with enlarged apices, with some setae apically and two lines of long, thick setae on flattened ventral side. All tarsal claws similar, narrowly cleft, with lower tooth longer and wider than upper tooth (Fig. 9). Genital capsule with parameres dorsally fused, ventrally notched, symmetrical, apex of each elongated, wide, and directed inward; margin of apical area covered with abundant, golden short setae, posteriorly more long; dorsal area bare, ventral area with numerous golden, decumbent, short setae. Aedeagus widely sclerotized forming a deeply channeled structure, with two dorsal, claw-shaped, laterally flattened, sclerotized projections fused basally (Figs. 10–12). Tectum large, longitudinally sulcated in apical half. Length of genital capsule from apex of parameres to border of basal piece: 4.9 mm. Total body length: 23.0 mm. Humeral width: 9.3 mm.

Allotype female: Similar to male except as follows: clypeus, frons and pronotum reddish brown; head with more fine punctures; antenna with lamellae of 8th to 10th segments slightly longer or equal to length of six preceeding segments combined.Visible abdominal sternites II to IV convex, V sternite large, transversely concave; anal plate short, convex, with various scattered setiferous punctures and few slender setae at posterior border. Pygidium convex, apical depression more deep and wide than male, apical border rounded, with 15 setae along apical border. Protibia with teeth of external border wider and longer than in male. Metatibia not flattened, with one oblique, sharp, setiferous carina on external side; dorsal border serrated; apical spurs articulated, similar length, lanceolate, upper straight, lower slightly curved (Fig. 13). Protarsus longer than protibia (1.42:1). Ventral genital plates moderately sclerotized, symmetrical, dorsal genital plates fused with central, longitudinal keel, and border bisinuated, centrally notched, with 8–10 setae on each side near border (Fig. 14). Total body length: 22.0 mm. Humeral width: 9.5 mm.

Variation.—*Male:* Similar to holotype except with more setae on abdominal sternites II–V; pygidium more strongly longitudinally rugose; pronotum more or less punctured; elytra more or less densely punctured; total body length: 21.5–22.0 mm; humeral width: 9.0–9.3 mm.

Type material.—Described from 7 ♂, 1 ♀. Holotype ♂ UVGC: Guatemala: Alta Verapaz, Purulhá, camino a Pantin, V-1995, J. Monzón. Allotype ♀ UVGC: same data as holotype. Paratypes: same data as holotype (1♂) (MXAL); Guatemala: Baja Verapaz, 19–24 km N Salamá, 1,500 m, 25/31-V-1989, J. E. Wappes (5 ♂) (UVGC, MXAL, UNSM).

Type locality.—Old road between Salamá and Purulhá, between departments of Alta Verapaz and Baja Verapaz, Guatemala (approx. 15°11′N; 90°18′W).

Biological data.—Males and female of *P. schusteriana* were collected at UV and Hg lights in pine-oak forests with *Liquidambar,* at 1,500 m altitude. Phenology: May (8).

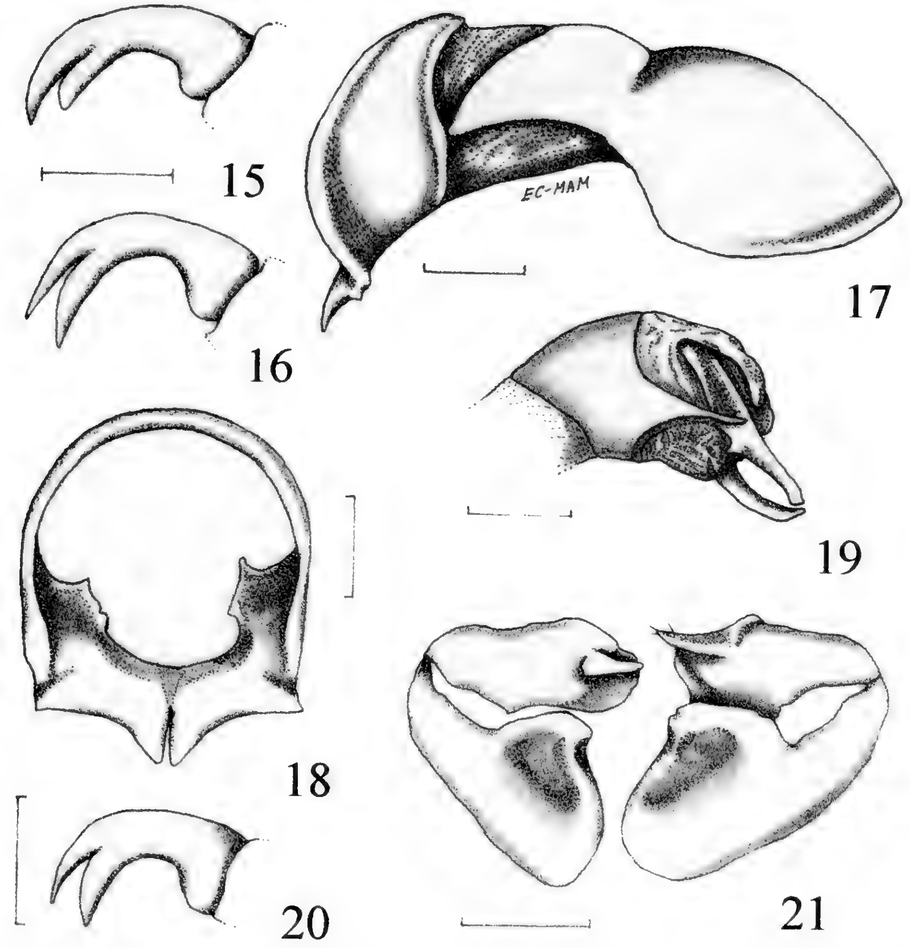
Remarks.—*Phyllophaga* (*Chlaenobia*) *schusteriana* is tentatively placed in the species group "*vexata*" (*sensu* Morón 1986). By body size, general vestiture, punctuation on the clypeus, pronotum, and elytra, it differs from other species of *Chlaenobia.* The structure and proportions of the parameres and aedeagus are clearly different from other species in the subgenus, and have some similarity with species in the subgenus *Phytalus,* such as *P. guatemala* Saylor. Also, the flattened shape of male metatibia of *P. schusteriana* is unique among the species of *Phyllophaga* (*s. lato*) with cleft tarsal claws.

Etymology.—This interesting species is named in honor of Dr. Jack C. Schuster, well known coleopterist, rock-folk musician, and acclaimed professor of biology.

Phyllophaga (*Chlaenobia*) *marilucasana* Cano and Morón, new species

(Figs. 15–21)

Description.—*Holotype male:* Clypeus yellowish testaceous, anterior border darker, frons and vertex reddish brown, frontoclypeal suture yellowish; pronotum shiny straw yellowish; elytra shiny straw yellowish without macroscopic vestiture; mouthparts, sterna, pygidium and legs shiny yellowish. Clypeus 2.87× wider than long, anterior border widely sinuate, with elevated margin, surface shiny, slightly irregular, slightly convex, with many uniformly distributed, shallow, rugose punctures, separated by 1 or less than 1diameter, each puncture with microscopic seta. Frontoclypeal suture sinuate and deeply impressed. Frons 1.80× wider than long, convex, with punctuation similar to clypeus, but deeper and concentrated toward posterior border.



Figs. 15–21. *Phyllophaga* (*Chlaenobia*) *marilucasana*. 15, Male protarsal claw, lateral view. 16, Male metatarsal claw, lateral view. 17, Genital capsule, lateral view. 18, Parameres, distal view. 19, Apex of aedeagus, laterodistal view. 20, Female protarsal claw, lateral view. 21, Female genital plates, ventral view. Scale lines = 1 mm, except figs. 15–16, 20 = 0.5 mm.

Vertex with small punctures on lateral border. Antenna 10-segmented, with 3-segmented club, lamellae narrower than length of basal segments combined (0.77:1). Frons 3.4× wider than dorsal diameter of each eye. Eye canthus long and narrow, with 8–9 setae. Labrum bilobed, deeply sinuate, with scattered long, slender setae on borders and across antero-superior border. Mentum slightly concave, impunctate, with scarce lateral setae, anterior border sinuate. Pronotum 1.92× wider than long and 2.6× wider than frons. Pronotal disk shiny, with round, shallow punctures, each with microscopic setae, scarcely separated, more abundant and with rugose aspect towards lateral and anterior margins; lateral borders widely angulated, lateral marginal bead almost entire, with scattered, short or long, slender setae; basal bead strongly indicated, except in front of scutellum indicated only by scarce punctures; anterior angles obtuse, not prominent; posterior angles not directed downward, obtuse. Scutellum 1.3× wider than long, with some minute punctures and 5 long, procumbent apical setae. Elytron 3.17× longer than wide, shiny, under great magnification tegument micro-rugose, nearly chagrinate, under low magnification surface densely rugo-punctate; punctures small and shallow, each with minute seta, separated by 1–2 diameters; epipleural border very wide at base, narrow along complete margin, with some scattered, short, slender setae; humeral callus rounded, prominent; apical callus rounded. Metathoracic wings completely developed. Propygidium shiny, yellowish with scattered, transversal punctuation and many minute decumbent and erect setae towards basal border. Pygidium very convex, shiny, strongly rugose, with visible some scattered shallow punctures regularly distributed, with rounded-conical prominence located near middle of preapical border, basal border without setae; apical margin with 13 long, slender setae; basal margin complete, preceeding by a shallow, transverse sulcus. Pterosternum with moderately dense, long yellowish setae. Visible abdominal sternites II to IV of similar length, slightly concave, minutely setose at middle; sternite V with wide transverse posterior sulcus, anteriorly with 4 long, slender setae near the middle; posterior border with marginal bead effaced at middle. Anal plate short, slightly concave at midline, posterior border thickened, notched at midline, with a few long erect setae along complete border. Protibia shorter than protarsus (0.72:1), with external border tridentate, proximal tooth poorly developed, almost imperceptible, preapical spur narrow, nearly straight, apex acute, half as long as 2nd protarsomere. Mesotibia with one oblique, sharp, setiferous carina on external side; upper apical spur straight, narrow, and 1.47× longer than lower spur. Metatibia shorter than metatarsus (0.59:1), with one oblique, sharp, setiferous carina on external side; upper apical spur articulated, curved, apex rounded to acute, slightly shorter than basal metatarsomere, and 1.47× longer than lower spur; lower apical spur articulated with tibial border, curved with rounded apex. Tarsomeres depressed, elongate, with enlarged apices, with some setae apically and two lines of long, thick setae on flattened ventral side. Protarsal claws narrowly cleft, with lower tooth shorter than upper tooth; meso- and metatarsal claws with lower tooth slightly shorter than upper tooth (Figs. 15–16). Genital capsule with large parameres, dorsally and ventrally fused, almost symmetrical, apex of each elongated, acute, tooth-like and directed downward, each with one asymmetrical laminar projection on internal face, directed upward. Aedeagus widely sclerotized with 2 lateral, narrow projections and lower apical, flattened, very sclerotized projections (Figs. 17–19). Tectum shortened, with dorsal depression near distal third. Length of genital capsule from apex of parameres to border of basal piece: 5.5 mm. Total body length: 17.5 mm. Humeral width: 7.0 mm.

Allotype female: Similar to male except as follows: antenna with lamellae of 8th to 10th segments equal to length of six preceeding segments combined. Visible abdominal sternites II to V convex, V sternite with setiferous punctures near middle; anal plate slightly convex, with many scattered setiferous punctures, and 11 slender setae at posterior border. Pygidium very convex, with 6 setae along apical border, without conical prominence, with 6 setae along apical border. Protibia with teeth of external border wider and longer than in male. Both apical spurs of metatibia articulated, wide, lanceolate and curved. Protarsus longer than protibia (1.26:1). Tarsal claws similar on all legs; lower tooth slightly longer than upper or equal in length (Fig. 20). Ventral genital plates sclerotized, nearly symmetrical, with complex combination of keels and sulci, surface with scattered minute setae; dorsal genital plates with a notable apical acute process with short setae on distal border (Fig. 21). Total body length: 19 mm. Humeral width: 9 mm.

Variation.—*Male:* similar to holotype except as follows: frontoclypeal suture reddish brown, mentum with 6–8 punctures. *Female*: similar to allotype, except apical process of dorsal plates less acute and less notable.

Type material.—Described from 3 ♂, 4 ♀. Holotype ♂ UVGC: Guatemala: Santa Rosa, Pueblo Nuevo Viñas, Finca Miramundo, 1,900 m, 10-VI-1999, J. Monzón y E. Cano. Allotype ♀ UVGC: same data as holotype. Paratypes: Guatemala: Sololá, Santa María Visitación, Sierra Parraxquim, 2,100 m, 3-V-2000, bosque nuboso, J. Ordoñez (CDC-CECON), col. (2♂) (MXAL, UVGC); same data except 6-V-2000 (2♀) (MXAL, UVGC); Guatemala: Sacatepequez, Antigua Guatemala, 1,600 m, 26-IV-2000, A.C. Bailey y J. Monzón (1♀) (UVGC).

Type locality.—Cerro Miramundo, department of Santa Rosa, Guatemala (approx. 14°12′N; 90°30′W), an extinct Quaternary strato-volcano.

Biological data.—Males and females of *P. marilucasana* were collected at UV and Hg lights in a pine-oak forest near a coffee plantation and an oak forest with some *Pinus, Ostrya,* and *Carpinus,* at 1,600–2100 m altitude. Phenology: April (1), May (4), June (2).

Remarks.—*Phyllophaga* (*Chlaenobia*) *marilucasana* belongs to the species group "*vexata*" (*sensu* Morón 1986). By body shape, size, color, general vestiture, punctuation on the clypeus, pronotum and elytra, as well as the general shape of male genital capsule, it is similar to *P.* (*Chirodines*) *zunilensis, P.* (*Chlaenobia*) *solanophaga, P.* (*Chlaenobia*) *ratcliffeiana,* and *P.* (*Chlaenobia*) *fraternaria,* but the detailed structure and proportions of the parameres and sclerotized accesories of the aedeagus are clearly different in all of these species. Also, the narrowly cleft hind tarsal claws separate it from *P. zunilensis* and the coarsely rugose pigydium and its preapical prominence separate it from *P. solanophaga* and *P. ratcliffeiana. Phyllophaga* (*C.*) *marilucasana* is allied to *P. fraternaria,* and it is difficult to separate them except by the male and female genitalia.

Etymology.—This species is dedicated to Maria Luisa Castillo, whose collecting efforts in many rotten logs have provided a large number of interesting samples of Melolonthidae and Passalidae.

New Country Records

Phyllophaga (*Chlaenobia*) *aegrota* (Bates).—Guatemala: Huehuetenango, Barillas, aldea Malpais, 1,200 m, VII-1998, bosque nuboso, E.Cano (6 specimens) (UVGC).

Phyllophaga (*Chlaenobia*) *scabripyga* (Bates).—Guatemala: Sacatepequez, Escuintla, finca Eminencia, Volcán de Agua, 1,400 m, 4-IV-2000, bosque nuboso. J. Monzón (16 specimens) (UVGC). Guatemala: Huehuetenango, Huehuetenango, aldea Chivacabé, 7-VI-1997, P. Alarcón (1♀) (UVGC).

Acknowledgments

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SABETHES (*PEYTONULUS*) *PARADOXUS*, A NEW SPECIES OF SABETHINI (DIPTERA: CULICIDAE) FROM PANAMA

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Abstract.—The male, pupa and larva of ***Sabethes* (*Peytonulus*) *paradoxus* Harbach, n. sp.**, are described and illustrated from Panama. The adult male lacks the brilliant metallic-colored scaling that is characteristic of all other *Sabethes,* and the paddle of the pupa is heterogeneous for the presence of a basal membranous area, a feature that has not been observed in other members of subgenus *Peytonulus.*

Key Words: Diptera, Culicidae, *Sabethes, Peytonulus,* new species, mosquito, Panama

When Hall et al. (1999) described *Sabethes luxodens,* subgenus *Peytonulus* Harbach included 11 formally named species and at least four unnamed species. The species described in this paper is one of the four previously unnamed species, the species which Harbach (1991) said "lacks metallic scutal scaling and bears certain other stasimorphic characters."

Species of subgenus *Peytonulus* are readily identified by unique apomorphies that include the remarkably modified seta 1-VII of larvae and the absence of its ontogenetic homolog in pupae. Nevertheless, like all groups of organisms, members of the subgenus exhibit combinations of both ancestral and derived features, and the species described herein is a striking example of this. While the species bears the apomorphic characters diagnostic of the subgenus, it exhibits the plesiomorphic condition of the scutal scaling that is characteristic of genus *Wyeomyia* Theobald. The derived position of *Sabethes* Robineau-Desvoidy relative to *Wyeomyia* is supported by the cladistic analysis of Harbach and Kitching (1998).

MATERIALS AND METHODS

This study is based on specimens borrowed from the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. Observations of the adults were made under simulated natural light. Larval and pupal chaetotaxy were studied using a combination of bright field and differential interference contrast microscopy. Measurements and counts were taken from all specimens of the type series where the structures in question were present. Numbers in parentheses represent modes of the reported ranges unless indicated otherwise. The form of presentation, descriptive terminology and abbreviations used in the description follow Harbach and Knight (1980, 1982) and recent papers published as part of an ongoing revision of genus *Sabethes* (Harbach and Peyton 1991; Harbach 1991, 1994, 1995a, 1995b; Harbach and Petersen 1992; Hall et al. 1999; Moses et al. 2000).

Sabethes (*Peytonulus*) *paradoxus* Harbach, new species

(Figs. 1–3)

Sabethes (*Sabethinus*) sp 2 of Heinemann and Belkin 1978: 193.

This species is unique in lacking the brilliant metallic-colored scaling that is characteristic of *Sabethes* (Harbach and Peyton 1991). The female is unknown. For the most part, the male resembles species of *Wyeomyia* in overall ornamentation, particularly the relatively dull coloring of the scutal scaling.

Male.—Relatively small species with broad, flat, distinctly metallic-colored scaling only on head, antepronota and thoracic pleura; scales of vertex with different combinations of metallic blue, violet and green reflections depending on angle of light; scales of postgena, thoracic pleura and coxae silvery white; antepronotum ranging from brown to bright blue and violet depending on angle of view, lower margin with few silvery white scales; scutum and scutellum densely covered with moderately broad dark scales with dull bluish reflections; mesopostnotum without scales; proboscis and legs predominantly dark-scaled with subdued blue and violet reflections when viewed from certain angles; wing with veins entirely dark-scaled, anterior veins darker with bluish sheen depending on angle of light; abdominal terga mainly dark-scaled with weak bluish, greenish and golden reflections, lateral margins with rather large rounded pale patches; sterna with yellowish-brown scaling. *Head:* Eyes joined above and below. Occiput with transverse row of short semi-erect scales at back of head. Ocular setae moderately long, dark, close to margin of eye; 2 long, bronzy, approximated interocular setae present. Antenna dark; length about 1.8 mm, slightly shorter than proboscis; pedicel large, surface pubescent, with inconspicuous fine setae on dorsomesal area; flagellum rather strongly verticillate, proximal whorls with 14 setae, longest setae about 0.4 length of antenna. Clypeus and frons without setae and scales, clypeus with dense covering of silvery pubescence. Proboscis short, length about 2.0 mm, longer than antenna, about 0.8 length of forefemur; distal 0.2 of prementum flattened, expanded laterally to 4 times width of proximal part and bent downward; ventral surface white-scaled beginning 0.2–0.4 from base and extending to expanded distal part, white scales grading to pale yellow at base of expanded part, dark scaling of expanded part distinctly darker (black), especially ventrally, than other dark scaling of prementum; labella short, very broad and dark-scaled proximally. Maxillary palpus short, 0.12–0.15 length of proboscis; dark-scaled, ventral surface without scales. *Thorax:* Integument brown. Dorsum with dark setae on anterior promontory (9–12), antepronotum (10–14), supraalar area (22–24), scutellum (6,7) and mesopostnotum (9–14). Pleura with 2 or 3 prespiracular setae, 2–5 upper proepisternal setae, 6–8 long lower mesokatepisternal setae extending well above ventral margin of mesepimeron and 11–14 upper mesepimeral setae; prespiracular setae dark, others yellow or golden. Lower part of proepisternum without scales, scales on upper part contiguous with scales on anteprocoxal membrane; scales absent from postprocoxal membrane; mesopleuron with scales except on lower anterior margin of mesokatepisternum, upper posterior margin of mesepimeron and mesomeron; scales absent from metapleuron, metameron and postmetacoxal membrane. *Wing:* Length 3.5 mm; scales on veins moderately broad and slightly asymmetrical, smaller on cubitus and anal vein; alula with fine piliform scales on margin distally; calypters without setae. *Halter:* Scabellum without scales, integument pale; pedicel and capitellum dark-scaled. *Legs:* Without paddles; coxae and trochanters with silvery-white scales, trochanters with some dark scales dorsally at apices; femora dark above and golden below; tibiae mainly dark with golden scaling proximally on ventral surface; tarsi entirely dark-scaled except ventral surface of hindtarsomere 5 white-scaled. Forefemur about 1.3 length of proboscis, same length to slightly shorter than midfemur, about 1.3 length of hindfemur; hindtibia about as long as hindfemur, hindtarsomere 1 longer than

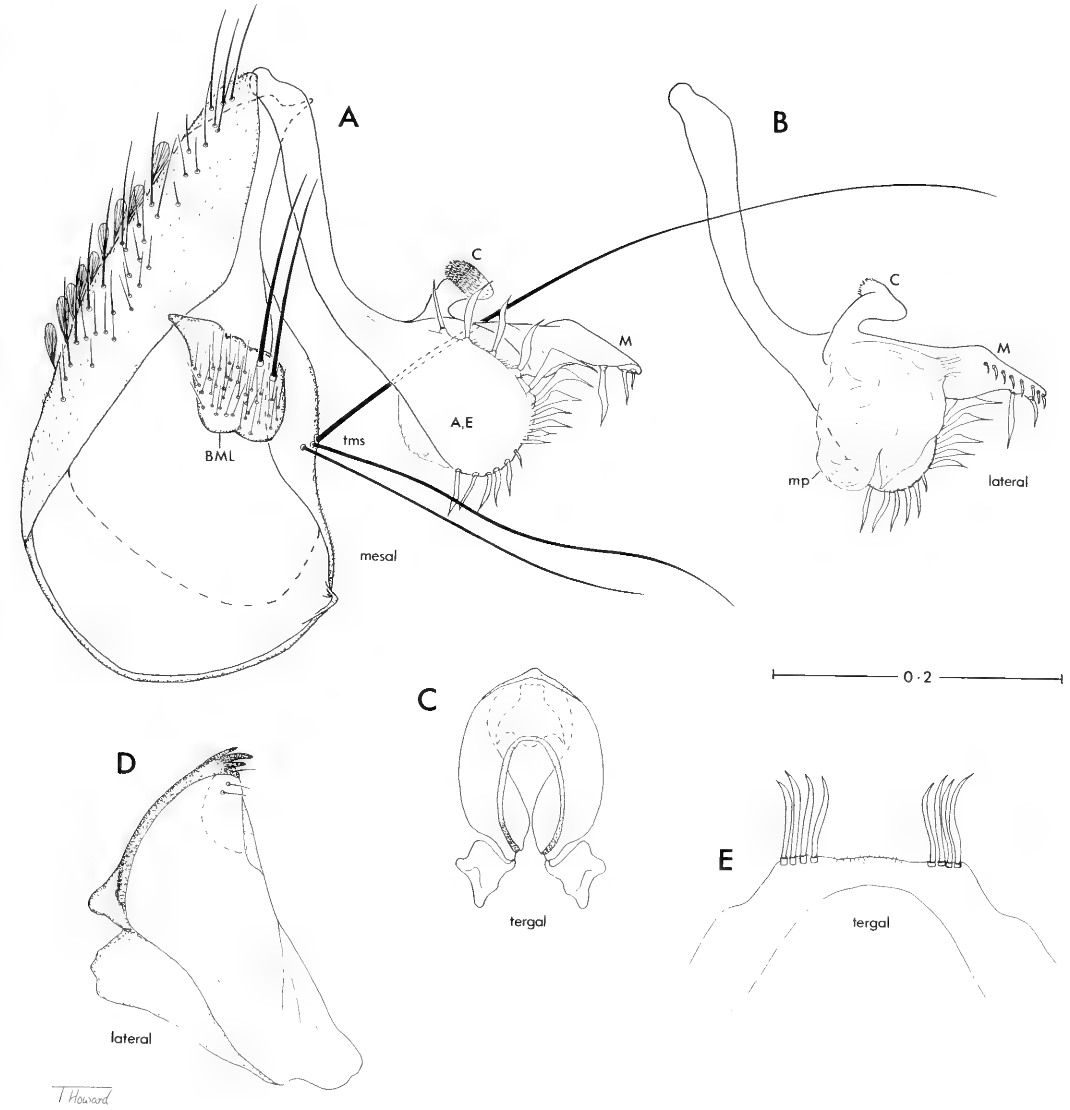

Fig. 1. Male genitalia of *Sabethes paradoxus,* aspects as indicated. A, Gonocoxopodite. B, Gonostylus. C, Aedeagus, with parameres attached. D, Proctiger. E, Tergum IX. Abbreviations: A, E, C and M = gonostylar lobes; BML = basal mesal lobe; mp = membranous process; tms = tergomesal setae. Scale in mm.

hindfemur. Ungues small, simple, black. *Abdomen:* Coloration as noted above; lateral pale areas of terga with silvery scales dorsally grading into yellow scales ventrally. *Genitalia* (Fig. 1): Tergum VIII (ventral in position; not figured) with posterolateral corners produced and broad V-shaped emargination at middle of posterior margin, border on either side of emargination with 4 or 5 irregular rows of long close-set setae extending to posterolateral corners, setae become longer and more numerous toward corners; scattered scales before and among setae; anterior 0.3–0.4 of tergum bare. Tergum and sternum IX fused laterally, forming a complete ring of sclerotization; tergum IX widely separated by relatively narrow bridge, lobes slightly produced, each with 4–7(5) flattened setae with apices bent laterad. Gonocoxite elongate, tapered in

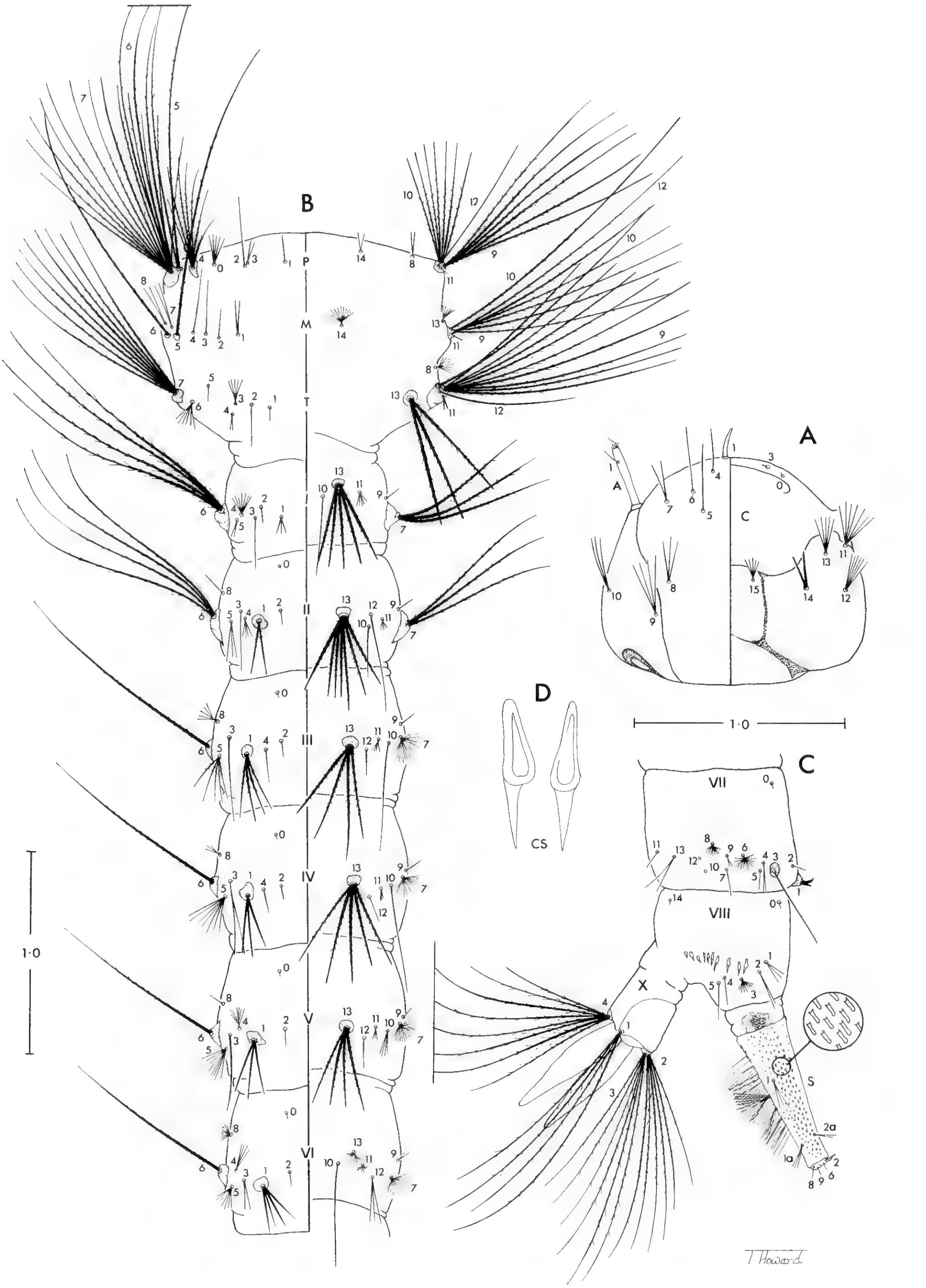

Fig. 2. Fourth-instar larva of *Sabethes paradoxus.* Reconstructed from exuviae of holotype; positions of setae may differ slightly from those shown. Setae missing from the right side of the exuviae (see Table 1) are drawn from those on the left side; an empty alveolus indicates that a seta was missing on both the right and left sides of the exuviae. A, Head, dorsal (left) and ventral (right) aspects of left side. B, Thorax and abdominal segments I–VI, dorsal (left) and ventral (right) aspects of left side. C, Abdominal segments VII–VIII and X, left

distal half, tergomesal surface membranous, distal part of sternal surface covered with scales and setae, bearing one very long and 2 unequal shorter tergomesal setae below level of basal mesal lobe; basal mesal lobe irregular in shape, produced caudomesally, covered with small slender setae and bearing 2 large setae at caudolateral angle. Gonostylus about 0.75 length of gonocoxite; stem narrow and curved in lateral view, slightly longer than head; head with 3 lobes developed as figured; lobe A,E large, laterally flattened and roughly ellipsoidal in lateral view, with fringe of setae from tergoapical angle to base of sternal side, setae on sternoapical edge noticeably flattened and expanded subapically; lobe M prominent, arising from sternolateral area of lobe A,E, tapered and bent apically, bearing 2 relatively large flattened setae on tergal margin and row of small stout setae on sternolateral surface; lobe C a relatively large stemmed process arising sternolaterally at base of head, bent mesad and bearing a globular head covered with rows of minute decumbent spicules; lateral side of head with a dangling bag-like membranous process (mp). Aedeagus longer than wide, broadly oval in tergal view; with submedian tergal arms joined at midline to form narrow median tergal bridge; apical tergal arms broadly fused and bearing a median tubercle; median sternal plate membranous, apex flared and hood-like. Proctiger (lateral view) with very broad basal sclerotization (tergum X) narrowly fused with base of paraproct; paraproct narrow, slightly enlarged apically, apex bearing 3 or 4 small teeth and 3 subapical cercal setae; cercal sclerite distinct.

Egg.—Unknown.

Larva, fourth instar (Fig. 2).—Reconstructed from single exuviae (holotype), character of setae as figured (positions may differ slightly from those shown), numbers of branches in Table 1. Exhibiting the subgeneric characters noted by Harbach (1991). *Head:* Slightly wider than long, widest in posterior half; length approximately 1.0 mm; width approximately 1.1 mm; moderately tanned. Occipital foramen widely V-shaped with arms extending dorsolaterally to point laterad of level of seta 9-C, margins heavily tanned, ventrocaudal margin with collar-like edge. Anterior margin of labiogula minutely denticulate; hypostomal suture complete, gently curved. Dorsomentum short, roughly triangular, with 8 teeth on either side of median tooth, median tooth and most lateral tooth of either side larger than the others. Mandible without distinctive features. Maxilla relatively short, with 4 large lateral teeth of nearly equal size, about 0.25 length of apical tooth; apical tooth large, about half length of maxillary body, curved mesad. Setae 4–6-C single, simple; 7-C double; 11,13-C relatively short, about length of 12-C; 14-C much thicker and stiffer than other cranial setae, double; 15-C inserted cephalad of 14-C near anterior margin of labiogula. *Antenna:* Short, cylindrical, length 0.3 mm; moderately tanned, progressively lighter toward apex, surface smooth. Seta 1-A single, simple, borne dorsally about 0.8 from base, length about twice width of antenna at point of insertion. *Thorax:* Integument hyaline, smooth. Setae 1-P,T, 4,5-T and 8,14-P weakly developed; 8-M much shorter than usual, slightly shorter than 7-M; 13-T shorter than thorax, with 3 thick aciculate branches. *Abdomen:* Integument hyaline, smooth. Setae 1-I weakly developed, 1-II-VI relatively well developed, with stiff thickened branches, borne on basal plates; 2-I-VII weakly developed, small

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side. D, Comb scales. Abbreviations: A = antenna; C = cranium; CS = comb scale; P = prothorax; M = mesothorax; S = siphon; T = metathorax; I–VIII, X = abdominal segments I–VIII, X; 0–15 = setal numbers for specified areas, e.g., seta 5-C. Scales in mm.

Table 1. Chaetotaxy of the fourth-instar larval exuviae of the holotype of *Sabethes paradoxus*. Number of branches of setae on the left and right sides of the body are separated by a slash. A question mark indicates that the number of branches could not be discerned. Missing setae are indicated by a short dash.

Seta	Head	Thorax			Abdominal Segments								
	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1/1	5/6	—	—	—	1/1	1/1	1/1	1/1	1/1	1/1	1/1	—
1	1/1	1/1	2/2	1/1	3/2	2/3	4/3	3/4	3/3	4/4	2/3	3/3	4/4
2	—	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	2/2	6/6
3	1/1	2/2	1/1	5/4	1/1	1/1	1/1	2/2	1/1	2/3	1/1	9/?6	6/6
4	1/1	8/7	1/1	2/2	7/5	4/6	1/1	1/1	7/7	4/4	2/2	1/–	8/8
5	1/1	2/2	1/1	1/1	2/2	3/4	5/6	7/4	8/6	7/11	1/1	1/2	—
6	1/1	3/–	1/1	6/6	4/4	4/4	1/1	1/1	–/1	1/1	14/–	—	—
7	2/2	12/12	2/2	8/9	3/3	3/3	21/20	?16/?	19/18	1/1	13/–	—	—
8	3/3	2/2	2/2	8/7	—	1/1	5/2	3/3	1/4	9/10	10/–	1-S,	3/2
9	4/4	6/6	5/5	9/11	1/1	1/1	1/1	1/1	1/1	2/1	2/2	1a-S,	3/3
10	3/3	7/6	1/1	1/–	1/1	1/1	1/1	1/1	4/3	1/–	–/–	2a-S,	2/2
11	7/6	1/1	1/1	2/2	?/5	6/6	4/5	3/3	3/4	11/8	1/1	—	—
12	6/5	1/1	1/1	1/1	—	1/1	1/1	1/1	1/1	3/2	–/–	—	—
13	5/5	—	6/7	3/3	5/5	7/7	4/5	5/3	4/4	–/14	2/2	—	—
14	2/2	2/–	10/8	—	—	—	—	—	—	—	1/1	1/1	—
15	5/6	—	—	—	—	—	—	—	—	—	—	—	—

and single, 2-I well laterad of 1-I, 2-II–VI well mesad and slightly anterior to seta 1; 6,7-I,II similarly developed but seta 6 significantly longer than seta 7, both strongly aciculate; 6-III–VI long, single, strongly aciculate; 7-III small, resembling 7-IV–VI, small with numerous branches; 9-I–VII all of normal size and development; 13-I–V well developed, stellate, with stiff aciculate branches, borne on basal plates; 4-III,IV distinctly mesad of seta 1, more or less midway between setae 1 and 2; 12-VI shorter than usual, double or triple; 11-VII ventral to seta 13-VII; 13-VII not strongly developed, double; punctures absent from segments III–V. *Segment VIII:* Comb an irregular single row of 10,11 small thorn-like scales without lateral fringes of minute spicules. *Siphon:* Short, tapered, slightly flared at apex; moderately tanned, with dark plates laterally at base; lateral surfaces covered with offset rows of blunt stud-like projections that decrease in length posteriorly; length 0.90 mm, width at base 0.35 mm, index 2.57. Pecten of approximately 70 filaments staggered irregularly along posterior margin, filaments arise individually (about 25) and in clusters, 2 large clusters at midlength arise from basal rings of paler integument that resemble alveoli, proximal of these clusters with 12 filaments, distal one with 6 filaments. Seta 1-S inserted about 0.4 from base. *Segment X:* Saddle lightly tanned, with imperceptible rows of minute spicules mainly on sides; length 0.22 mm; siphon/saddle index 4.1. Setae 1–4-X equally well developed, shorter than usual, multiple with aciculate branches.

Pupa (Fig. 3).—Character and positions of setae as illustrated, numbers of branches in Table 2. *Cephalothorax:* Lightly to moderately tanned, some darker mottling on scutum. Seta 1-CT strongly developed, double or triple, branches not noticeably sigmoidally curved, with hooked tips; 5-CT also well developed, single or double. *Trumpet* (Fig. 3A,C): Moderately and evenly tanned, short, rather abruptly expanded at base; length 0.38–0.47 ($\bar{x}$ = 0.43 mm), width at midlength 0.14–0.16 mm ($\bar{x}$ = 0.15), index 2.38–3.21 ($\bar{x}$ = 2.95); pinna short, length 0.06–0.11 mm ($\bar{x}$ = 0.09). *Abdomen:* Lightly to moderately tanned, sterna II–VII darker anteriorly; length 4.09–5.20 mm ($\bar{x}$ = 4.45 mm). Seta 5-I laterad of seta 4-I; 7-I shorter than seta 6-I, with 2–4 branches; 2-II anterolateral to 1-II; 3-II on level anterior to level of 2-II; 5-II,III much smaller than 5-IV–VI, 5-IV–VI longer than length of following tergum; 7-II dorsal to 9-II; 8-II present or absent, alveolus present when seta absent, 8-VI dorsal; 10-II present; punctures absent from segments III–V. *Genital lobe:* Lightly tanned, length (male only) about 0.6 mm. *Paddle:* Lightly tanned, broadest at base, narrowed apically, outer part wider than inner part, minutely spiculate along margins, demarcated basal membranous area present (Fig. 3D) or absent (Fig. 3B) on dorsal surface; length 0.59–0.70 mm ($\bar{x}$ = 0.66 mm), width at widest point 0.39–0.46 mm ($\bar{x}$ = 0.43 mm), index 1.46–1.65 ($\bar{x}$ = 1.52).

Systematics.—The female of *Sabethes paradoxus* is unknown, but the male is easily distinguished from that of all other species of the genus by the absence of brilliant metallic-colored scutal scaling, the greatly expanded apical portion of the proboscis, and features of the gonostylus. Assuming that the female of this species resembles the male in general habitus, it is possible, if not likely, that it will be confused for species of *Wyeomyia.* It will be necessary to note the absence of prealar setae to correctly identify the female as a species of *Sabethes.*

The larva of *Sa. paradoxus* most closely resembles that of *Sa. soperi* Lane and Cerqueira, but is easily distinguished from this and all other *Sabethes* by the short, uniquely ornamented siphon. Within subgenus *Peytonulus,* the robust development of seta 14-C is shared with *Sa. soperi* as well as *Sa. hadrognathus* Harbach and *Sa. undosus* (Coquillett). As far as known, the reduced seta 8-M of *Sa. paradoxus* is a unique feature of this species.

The pupae of *Peytonulus* are generally

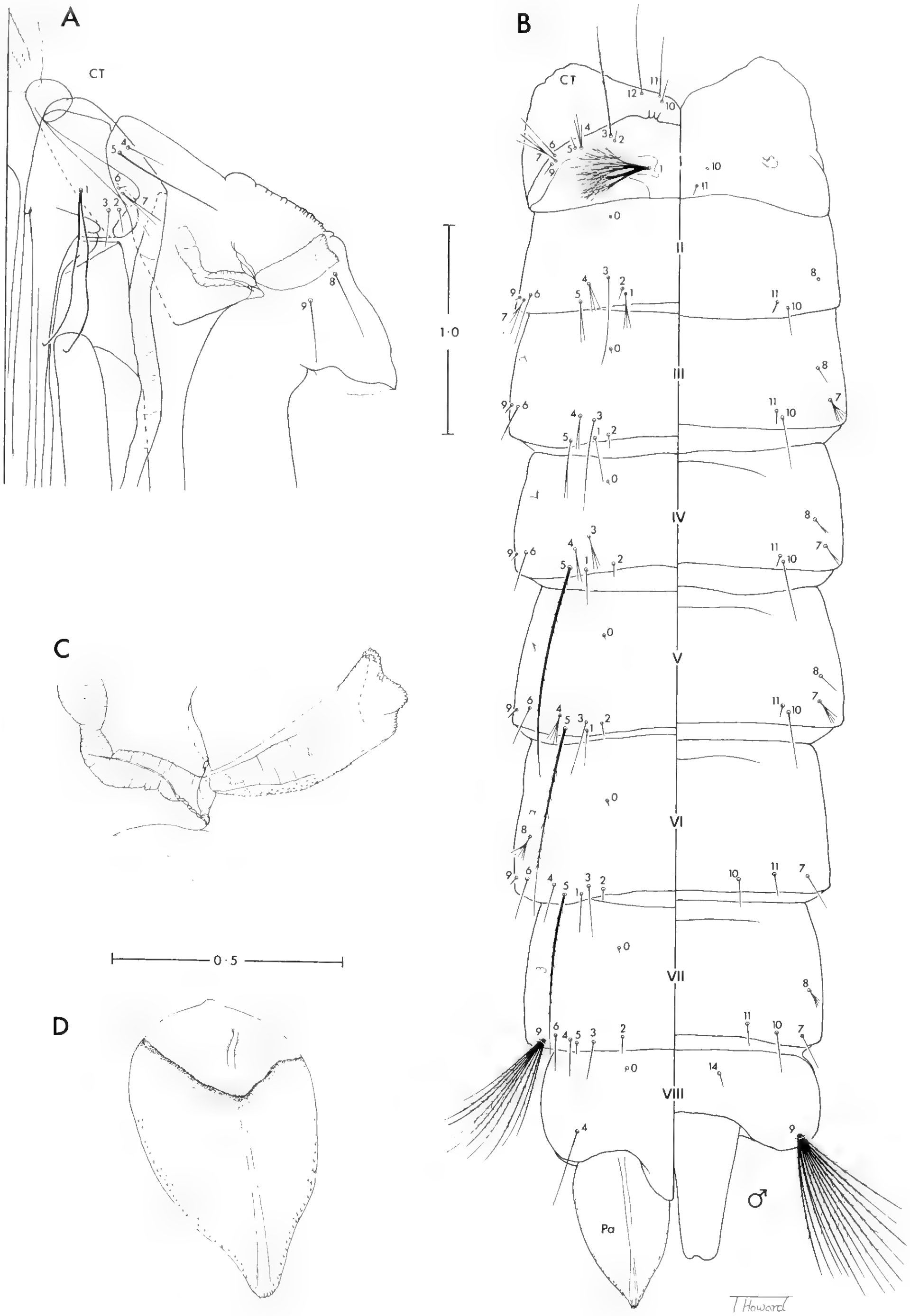

Fig 3. Pupa of *Sabethes paradoxus*. A, Left side of cephalothorax, dorsal to right. B, Dorsal (left) and ventral (right) aspects of metathorax and abdomen. C, Trumpet. D, Paddle of paratype GG105-121 showing basal membranous area of dorsal surface. Abbreviations: CT = cephalothorax; Pa = paddle; I–VIII = abdominal segments I–VIII; 0–14 = setal numbers for specified areas, e.g. seta 3-I. Scales in mm.

Table 2. Numbers of branches for setae of pupae of *Sabethes paradoxus*. Range (mode, when evident) of the type series (holotype and three paratypes).

	Cephalo-thorax	Abdominal Segments									Paddle
Seta	CT	I	II	III	IV	V	VI	VII	VIII	IX	Pa
0	—	—	1	1	1	1	1,2(1)	1	1	—	—
1	2,3(2)	38–45	1–4	1,2(1)	1,2(1)	1	1,2(1)	—	—	—	—
2	1,2(1)	1	1,2(1)	1	1	1	1	1	—	—	—
3	1,2	1	1	1	2–5(3)	1	1	1	—	—	—
4	1	1–3(3)	2–4(3)	1–3(2)	1–3(2)	2–7(4)	1	1	1	—	—
5	1,2	1–3(1)	1–4(2)	2–4(3)	1	1	1	0[a]/1(0[a])	—	—	—
6	1,2(2)	1	1	1	1,2(1)	1	1	1,2(1)	—	—	—
7	1–3(2)	2–4(2)	2–5(3)	3–7(5)	1,2(1)	2–5(4)	1,2(1)	1	—	—	—
8	1	—	0[a],1(0[a])	1,2	1–3(1)	1–4(1)	4–8(5)	3–7(4)	—	—	—
9	1	1,2(1)	1	1	1	1	1	9–14	11–15	—	—
10	1,2(1)	0[a]	1	1	1,2(1)	1	1	1	—	—	—
11	1	1	0[a]/1(1)	1	1	1	1	1	—	—	—
12	1	—	—	—	—	—	—	—	—	—	—
13	—	—	—	—	—	—	—	—	—	—	—
14	—	—	—	—	—	—	—	—	1	—	—

[a] Alveolus present.

very similar and more difficult to differentiate than the larvae. The pupa of *Sa. paradoxus* resembles that of *Sa. hadrognathus* and differs from other species of the subgenus in the dorsal placement of seta 8-VI. This seta is usually but not always dorsal in the latter species, and whether this is a fixed feature of *Sa. paradoxus* will remain uncertain until additional material becomes available for study.

The three paratypes of *Sa. paradoxus* (see below) were reared from pupae collected from bamboo. The pupal exuviae of one of these specimens (GG105-121) bears a differentiated membranous area at the base of the paddle. This is paradoxical for two reasons: the holotype and other paratypes have a normal paddle, and the feature is not known to occur in any other species of *Peytonulus*. A membranous area at the base of the paddle is characteristic of subgenus *Sabethoides* and occurs in some species of subgenus *Sabethes* (Harbach 1991). The exuviae does not appear to be incorrectly associated with the adult male because seta 8-VI is dorsal in position and the specimen otherwise agrees with the holotype and other paratypes in all other features. Seta 8-VI is ventral in species of subgenus *Sabethoides* and those species of subgenus *Sabethes* that have a membranous area at the base of the paddle. The genetics that control the expression of the character are unknown, but it seems plausible that this involves latent genes that may be influenced by environmental conditions. The function of the membranous area is likewise unknown, but it could be a region of weakness to facilitate abscission of the paddle should it be grasped by a predator or entangled in debris.

Etymology.—The specific name of *paradoxus* is a Latin adjective (masculine) meaning strange or contrary to expectation. The name refers to the uncharacteristic coloration of the adult male and the enigmatic presence of a delineated membranous area in one pupa of the type series.

Bionomics.—The holotype was collected as a larva found in a terrestrial bromeliad; the paratypes were collected as pupae found in bamboo. In addition to the holotype, the bromeliad also contained larvae of the *Culex* (*Microculex*) *imitator* group, *Johnbelkinia ulopus* (Dyar and Knab), *Limatus durhamii* Theobald, a species of *Toxorhynchi-*

tes (*Lynchiella*), a species of *Wyeomyia* (*Hystatomyia*), and two species of the *Wy.* (*Wyeoymia*) *pertinans* group. Species found in bamboo with the paratypes include the following (superscript 1 indicates collection GG105; 2 indicates collection GG109): *Culex* (*Carrollia*) *antunesi* Lane and Whitman[1,2], an unidentified species of *Cx.* (*Culex*)[1], *Limatus durhamii*[1], *Onirion sirivanakarni* (Duret)[1,2], *Sa.* (*Peytonulus*) *identicus* Dyar and Knab[1,2], *Sa.* (*Pey.*) *hadrognathus*[1,2], a species of *Shannoniana*[1,2] (same species in both collections), *Trichoprosopon pallidiventer* (Lutz)[2], *Tr.* sp. near *pallidiventer*[1,2], *Tr. castroi* Lane and Cerqueira[2], a species of *Tx.* (*Lynchiella*)[1] (?same species found in bromeliad), and two species of *Wyeomyia* (*Wyeomyia*)[1,2] (same two species in both collections). Nothing is known about the biology of the adults.

Distribution.—Known only from the type locality in the Darien of Panama. The species probably occurs in neighboring countries in Central America and northern South America.

Material examined.—Thirteen specimens (4 ♂, 4 ♂ genitalia, 1 larval exuviae, 4 pupal exuviae) from 1 larval and 3 pupal rearings. Holotype: ♂ (GG108-101, with associated larval and pupal exuviae and dissected genitalia on separate microscope slides), PANAMA: *Darien*, specific locality not known, 7 Jul 58, terrestrial bromeliad (Gorgas Memorial Lab. personnel). Paratypes, same data as holotype except as follows: 1 ♂ (GG105-121, with associated pupal exuviae and dissected genitalia on separate microscope slides), Pucro, 'Paya Camp', 50 m, 6 Jul 58, bamboo; 2 ♂ (GG109-112 and −122, both with associated pupal exuviae and dissected genitalia on separate microscope slides), Pucro, 50 m, 8 Jul 58, bamboo. The holotype and paratypes are deposited in the USNM.

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DESCRIPTION OF A NEW SPECIES OF THE GENUS *MASAAKIA* TAKEUCHI (HYMENOPTERA: TENTHREDINIDAE) FROM JAPAN

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Abstract.—***Masaakia katayamai,* new species**, from Honshu, Japan, is described and illustrated, and a key is provided for the three Japanese species of *Masaakia.*

Key Words: Symphyta, Tenthredinidae, Blennocampinae, *Masaakia,* new species, Japan

Masaakia Takeuchi is a small genus of the subfamily Blennocampinae and is endemic to Japan. It contains two described species, *M. longivaginata* Takeuchi 1950 and *M. shinoharai* Togashi 1998. Recently, I received two specimens of *Masaakia* through the courtesy of Mr. E. Katayama, Ohtawara City, Tochigi Prefecture, Honshu, Japan. These two specimens are distinguished from the two described species by the yellow tegula, shape of the pedicel, shape of the sawsheath, and the serrulae of the lancet. Thus, I concluded that these specimens represent a new species. Here, I describe and illustrate this new species and give a revised key to the Japanese species of the genus.

KEY TO THE JAPANESE SPECIES OF *MASAAKIA*

1. Apex of sawsheath pointed in lateral view (Fig. 11); tegula black; pedicel longer than wide (Fig. 10) 2
– Apex of sawsheath truncate in lateral view (Fig. 8); tegula yellow; pedicel shorter than wide (Fig. 4) . . . . *katayamai,* n. sp.
2. Antenna entirely black; radial crossvein of forewing curved . . . . *longivaginata* Takeuchi
– Antenna black with undersides of 4th to 9th segments and apical half of underside of 3rd antennal segment reddish brown; radial crossvein of forewing nearly straight (as in Fig. 5) . . . . *shinoharai* Togashi

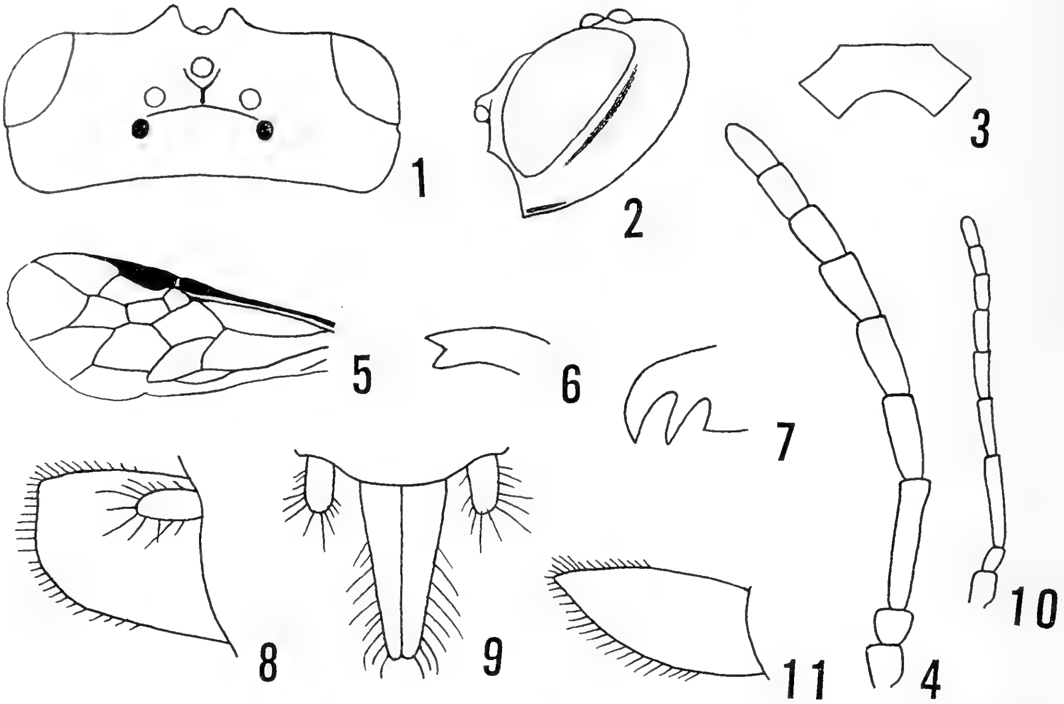
Masaakia katayamai Togashi, new species

(Figs. 1–9, 12, 13)

Female.—Length, 5 mm. Body including antenna black, but apical half of mandible reddish brown and tegula yellow. Wings hyaline; stigma and veins dark brown to black. Legs black with following parts milky white: tibiae except for apical portion and hind basitarsus.

Head from above transverse (Fig. 1); postocellar area transverse, slightly convex: OOL:POL:OCL = 1.1:1.0:0.9; posterior half of circumocellar furrow distinct, anterior half indistinct; interocellar and postocellar furrows distinct; lateral furrows distinct and deep, circular (Fig. 1); frontal area nearly flattened; median fovea distinct and deep, circular, with short longitudinal furrow in middle; lateral fovea distinct and deep, circular, with a small conical-like projection in middle; supra-antennal tubercles distinct; antenno-ocular distance about twice as long as distance between antennal sockets; front margin of clypeus emarginate (Fig. 3); malar space narrow, 0.2× as long as diameter of front ocellus; postorbital groove distinct (Fig. 2); postgenal carina distinct near mandible only (Fig. 2).

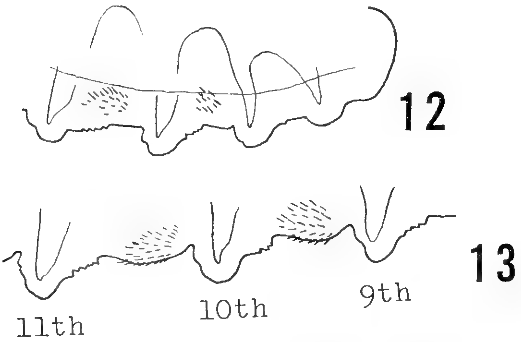
Antenna (Fig. 4) shorter than costa of forewing; relative lengths of segments about 1.6:1.0:4.7:2.6:2.6:2.3:1.6:1.6:2.0;



Figs. 1–11. 1–9, *Masaakia katayamai,* holotype. 1, Head, dorsal view. 2, Head, lateral view. 3, Clypeus, front view. 4, Antenna, lateral view. 5, Forewing. 6, Fore inner tibial spur, lateral view. 7, Tarsal claw, lateral view. 8, Sawsheath, lateral view. 9, Sawsheath, dorsal view. 10–11, *M. longivaginata.* 10, Antenna, lateral view. 11, Sawsheath, lateral view.

pedicel rectangular, length to width about 1.0:1.3 (Fig. 4).

Thorax with mesoscutellum slightly convex; epicnemium absent. Forewing with radial crossvein (2r) nearly straight (Fig. 5); vein 2A+3A straight. Hindwing with petiole of anal cell about twice as long as nervulus; cell M absent. Legs with fore inner tibial spur furcate at apex (Fig. 6); hindbasitarsus nearly as long as length of following 2 segments combined; tarsal claws with long inner tooth and basal lobe (Fig. 7).



Figs. 12–13. *Masaakia katayamai,* paratype. 12, Apical portion of lancet. 13, 9th to 11th serrulae of lancet.

Abdomen with sawsheath rather long (Fig. 9) in dorsal view, apical portion truncate in lateral view (Fig. 8); cercus short, 0.4× as long as sawsheath. Lancet with 16 serrulae, serrulae lobelike, rounded at apices; apical portion of lancet as in Fig. 12; 9th to 11th serrulae as in Fig. 13.

Head and thorax covered with fine setigerous punctures, those of clypeus closer than those on vertex; mesopleuron practically impunctate, shining. Abdominal tergites nearly impunctate.

Male.—Unknown.

Food plant.—Unknown.

Types.—Holotype ♀, 12.IV.2000, Yoichi, Ohtawara City, Tochigi Prefecture, E. Katayama leg. Paratype, 1 ♀, 29.IV.2000, Shimoishigami, Ohtawara City, Tochigi Prefecture, E. Katayama leg. Both deposited in the collection of the National Science Museum (Natural History), Tokyo.

Remarks.—This new species comes out to *Masaakia* in the keys to genera by Takeuchi (1952) and Okutani (1972). There are two minor discrepancies with the generic concept of *Masaakia,* the broad almost square pedicel and the shorter sawsheath with the apex truncated in lateral view. The typical species of *Masaakia* have the pedicel elongate, longer than broad, and the sawsheath longer and more pointed at its apex in lateral view. Other characters, however, support the placement of *M. katayamai* in *Masaakia,* e.g., the bifid tarsal claws with a basal lobe, third antennal segment longer than the fourth segment, emarginate clypeus, narrow malar space, short genal carina, presence of a hind orbital groove, lack of an epicnemium, straight vein 2A+3A of the forewing, and petiolate anal cell and absence of cell M of the hindwing.

Masaakia katayamai is similar to both *M. longivaginata* and *M. shinoharai,* but it is distinguished by the yellow tegula (in *M. longivaginata* and *M. shinoharai,* the tegula is black), by the broad pedicel (elongate in the other two species, compare Figs. 4, 10), by the truncate sawsheath (pointed at the apex in the other two species, compare Figs. 8, 11), and by the deeper, more rounded serrulae of the lancet (shallower and flatter in the other two species, compare Figs. 12, 13 and Togashi 1998, figs. 15, 16).

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A REVIEW OF *CHALODETA* STICHEL WITH A REVISION OF THE *CHELONIS* GROUP (LEPIDOPTERA: RIODINIDAE)

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Abstract.—An overview of the Neotropical riodinid genus *Chalodeta* Stichel is presented which defines the taxon, delineates its member species, and discusses its systematic position within the tribe Riodinini. A revision of the *Chalodeta chelonis* group includes notes on the taxonomy and biology of its species, and illustrations of the adults and male and female genitalia (where known) of all taxa. Four species are recognized, including two that are previously described, *C. chelonis* (Hewitson 1866) and *C. chaonitis* (Hewitson 1866), and two that are described here, ***C. chitinosa*, n. sp.**, and ***C. chlosine*, n. sp.** The taxon *stilbos* Stichel 1910, is synonymized with *C. theodora* (C. and R. Felder 1862) (**n. syn.**).

Key Words: *Chalodeta, Charis,* Neotropics, Riodinini, taxonomy

The monophyly of most genera in the Riodinidae has never been critically assessed, but to do so is vitally important if the family's classification is to become a predictive tool in broader evolutionary studies. The purpose of this paper is twofold. The first is to provide an overview and diagnosis for the small riodinid genus *Chalodeta* Stichel 1910, which has historically often been confused with other genera in the tribe Riodinini (*sensu* Harvey 1987), particularly *Charis* Hübner [1819], delineate its constituent species, and discuss its systematic position, biogeography, and biology. *Chalodeta* is hypothesized here to consist of two monophyletic groups, and the second purpose of this paper is to present a revision of one of these, the *chelonis* group, whose true species diversity has previously gone undetected. It consists of two named species, *C. chelonis* (Hewitson 1866) and *C. chaonitis* (Hewitson 1866), and two additional species, widely sympatric with *C. chaonitis,* that are described here. All four *chelonis* group species are illustrated here, while adequate color figures of all *theodora* group species may be found in d'Abrera (1994) (*C. theodora* (C. and R. Felder 1862) and *C. lypera* (Bates 1868)) and Hall and Willmott (1998) (*C. pescada* Hall and Willmott 1998 and *C. panurga* Stichel 1910).

Methods

Dissections were made using standard techniques, abdomens being soaked in hot 10% potassium hydroxide solution for approximately five minutes, and subsequently stored in glycerol. Specimens dissected are indicated in the material examined sections with an asterisk. Morphological terms for genitalia follow Klots (1956) and Eliot (1973), and the terminology for wing venation follows Comstock and Needham (1918). The protocol for listing material examined follows Hall (1999).

Chalodeta chelonis group specimens have been examined and their locality data recorded in the following collections, whose acronyms are used throughout the text. Only locality data are given in the species accounts of described taxa, but full label data are given for new species.

AME	Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, U.S.A.
BD	Collection of Boyce Drummond, Florissant, CO, U.S.A.
BMNH	The Natural History Museum, London, U.K.
JHKW	Collection of Jason Hall and Keith Willmott, Washington, DC, U.S.A.
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
RPM	Reading Public Museum, Reading, PA, U.S.A.
SMF	Senckenberg Museum, Frankfurt, Germany
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.
ZMHU	Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany
ZSM	Zoologische Staatssammlung, Munich, Germany

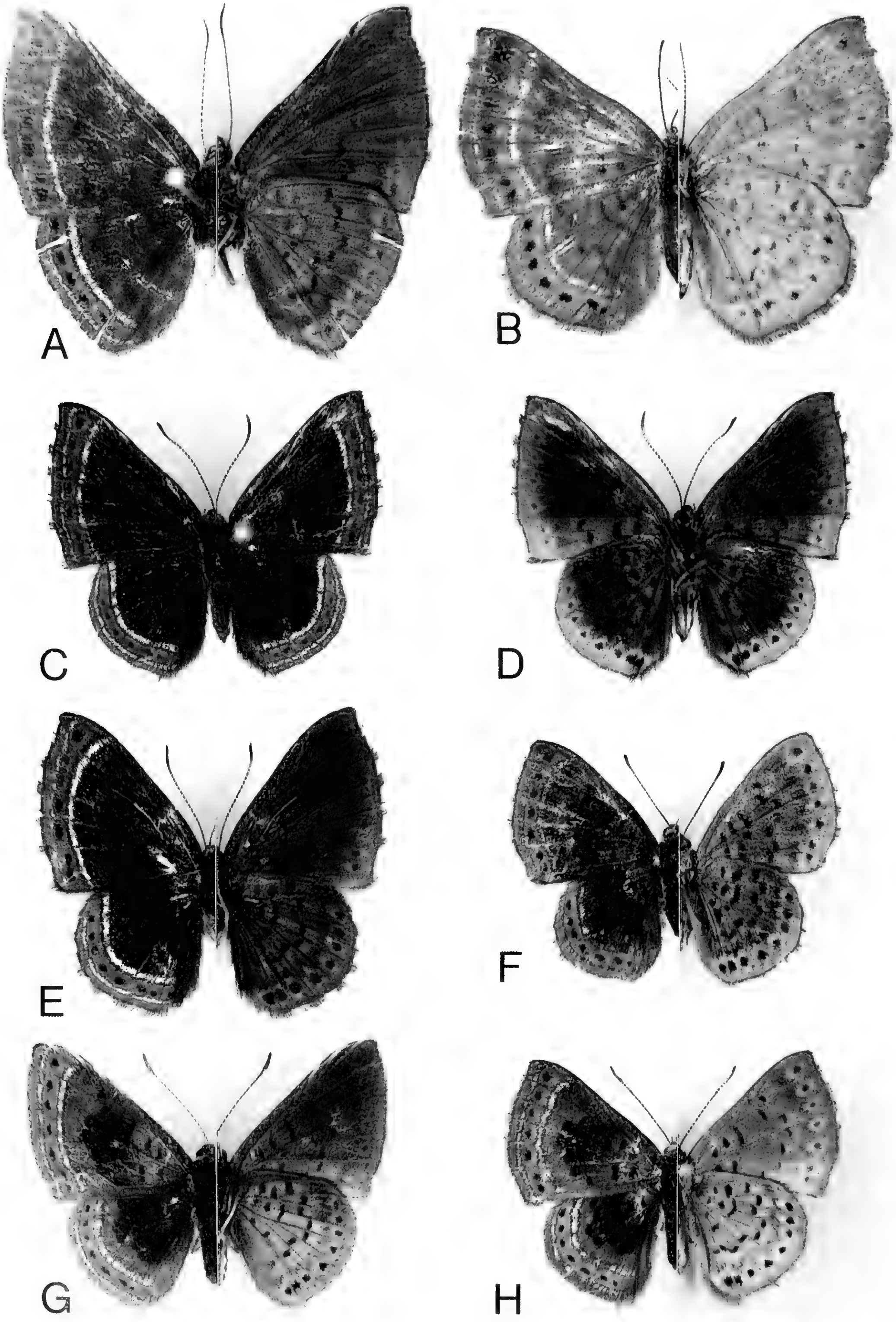
REVIEW OF *CHALODETA*

Chalodeta Stichel 1910

Chalodeta Stichel 1910b: 15. Type species by original designation: *Charis theodora* C. and R. Felder 1862: 72.

Diagnosis and systematic position.—*Chalodeta* species are small to medium-sized riodinids (forewing length 10 mm [*theodora*] to 16 mm [*chelonis*]) with compact wing shapes, often slightly falcate forewing apices, and rounded hindwings. The dorsal surface is typically brown with one (all *theodora* group species except *theodora*) or two (all *chelonis* group species and *theodora*) submarginal blue or greenish silver lines, three dark brown markings in the discal cell, and discal, postdiscal and submarginal bands of dark brown spots. The ventral surface is typically iridescent blue or purple in males and brown in females and has similar markings to the dorsal surface except no silver submarginal lines are present (see Figs. 1A–H). The fringe of both wings is often entirely white. All members of the often confused genus *Charis* except the misplaced *ocellata* group (Hall and Harvey, in prep.) have two dorsal submarginal silver lines, and all except one have some ventral submarginal silver markings. The exception is a recently described member of the *Charis gynaea* group (Hall and Harvey 2001), which was figured by DeVries (1997) as "*Chalodeta candiope*" and presumably placed by him in *Chalodeta* because of its lacks of ventral silver markings.

The male genitalia of all *Chalodeta* species (see Figs. 2A–D, 3) possess the deep notch in the anterior margin of the tegumen characteristic of the tribe Riodinini. The uncus is rectangular and in *chelonis* group species typically forms a small bifurcate posterior projection medially along the dorsal margin. The falces and tegumen are of average size and shape for the tribe, and the vinculum is evenly narrow and somewhat arched medially. The aedeagus is characteristically short, narrow and straight, unlike that of *Charis* and most other riodinine species, in which it is long and variably asymmetrically curved; no cornuti are present. The structure of the posteriorly elongate pedicel is unique. It is tightly appressed to the aedeagus, its tip forms a ventrally directed plate, and its basal ventral margin is unsclerotized. The ventral tip contains elongate spines around its perimeter in *chelonis* group species, but only very small spines (*lypera* only) or no spines in *theodora* group species. The valvae of the two *Chalodeta* species groups are very distinct.


A
B
C
D
E
F
G
H

Those of the *chelonis* group (Fig. 2) have a small narrow lower process that is unsclerotized at its base and a posteriorly elongate upper process that typically has a medial dorsal projection and long broad spines at the tip of both upper projections (only *chitinosa* lacks a dorsal upper process). The transtilla is connected to the upper valve process only at its base and is narrow and very posteriorly elongate with two upwardly curving brachia at its tip. Valvae of the *theodora* group (Fig. 3; see also male genital illustration of *C. pescada* in Hall and Willmott 1998) have an entirely sclerotized lower process and an upward and slightly outwardly directed upper process with no spines. The transtilla is connected to the upper valve process along its entire length, creating a broad concave dorsal plate that narrows to a small bifurcate and grooved tip within which the tip of the aedeagus is confined.

The female genitalia (see Figs. 4A–C) differ slightly between the two species groups. Those of the *chelonis* group have an elongate corpus bursae with elongate invaginated spine-like signa and a large area of sclerotization on the eighth abdominal sternite that is often medially desclerotized. The known females of the *theodora* group have a rounded corpus bursae with the signa either forming rectangular invaginations with an elongate base at the wall of the corpus (*theodora*) or two sclerotized bands at the wall of the corpus (*lypera*), and a small area of sclerotization on the eighth abdominal sternite. In all species, the ductus bursae is relatively short and unusual in extending to the dorsal tip of a posteriorly elongate ostium bursae. The position in all *Chalodeta* species of the small ventral sclerotized plate in the ductus bursae at the opening of the corpus bursae instead of immediately before the ostium (creating an elongate ductus seminalis parallel to the ductus bursae) is not known elsewhere in the tribe.

As indicated above, despite a superficial external similarity (including the possession of hairy eyes), the genital morphology does not suggest a particularly close relationship between *Chalodeta* and *Charis* within the Riodinini, although the presence of most wing pattern elements in the species of these genera suggests they are both relatively basal within the tribe. Currently very little is known about relationships between genera in the Riodinini and what makes the pursuit of this knowledge all the more difficult is the relative lack of conservative characters. While the tremendous interspecific variation in genitalia provides good diagnostic characters at the species and species-group levels, it acts to confound the elucidation of relationships at the generic level and above. The other putatively basal riodinine genera which still possess most wing pattern elements are *Metacharis* Butler 1867, *Dachetola* Hall 2001, *Calephelis* Grote and Robinson 1869, *Caria* Hübner 1823, *Amphiselenis* Staudinger 1887, *Lasaia* Bates 1868, and *Exoplisia* Godman and Salvin 1886. However, the male genitalia of all but the first two of these genera possess pedicels tipped with the typical riodinine scobinate patch. *Chalodeta* may be most closely related to *Metacharis* and *Dachetola,* which possess a somewhat similar wing pattern devoid of ventral silver, and a posteriorly elongate "rod"-like pedicel and a simple strap-like pedicel respectively.

History of classification.—Stichel (1910a) described the genus *Chalodeta* to

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Fig. 1. *Chalodeta* adults (dorsal surface on left, ventral surface on right, unless otherwise stated). A, ♂ *C. chelonis,* Petrópolis, S.E. Brazil (USNM). B, ♀ *C. chelonis,* Petrópolis, S.E. Brazil (USNM). C, Holotype ♂ *C. chlosine,* dorsal surface, Pakitza, Peru (USNM). D, Holotype ♂ *C. chlosine,* ventral surface. E, Holotype ♂ *C. chitinosa,* Tingo Maria, Peru (USNM). F, Allotype ♀ *C. chitinosa,* Pakitza, Peru (USNM). G, ♂ *C. chaonitis,* Parque do Gama, S.E. Brazil (USNM). H, ♀ *C. chaonitis,* Parque do Gama, S.E. Brazil (USNM).

include the species *theodora, lypera, panurga, chaonitis,* and *calagutis* Hewitson 1871, designating the first of these as the type species, but subsequently added *chelonis, epijessa* Prittwitz 1865, *azora* Godart [1824] (Stichel 1910b) and *speusippa* Schaus 1928 (Stichel 1930–31). The taxon *virido* Lathy 1958, was added to *Chalodeta* by Rebillard (1958) as a subspecies of *chelonis,* but subsequently raised to species rank by Callaghan (1995). In his first riodinid catalog, Bridges (1988) placed *calagutis* in *Charis,* presumably inadvertently, although *calagutis* and the remaining members of the *ocellata* group are actually generically distinct from *Charis* (Hall and Harvey, in prep.). d'Abrera (1994) confused the generic status of *Chalodeta* by combining it with *Charis* in his pictorial overview of the family, stating: "Some workers follow Stichel (1910) in separating certain species in this group into the genus *Chalodeta* Stichel, 1910. . . . This writer considers this confusing and unnecessary and will retain them all in *Charis* Hübner." However, Bridges (1994) retained *Chalodeta* distinct from *Charis.* Most recently, DeVries (1997) synonymized *speusippa* with *lypera,* Hall and Willmott (1998) described *pescada,* and Hall (2001) transferred *virido* and *azora* (with *epijessa* as a synonym) to *Dachetola.* Since two species are newly described here, I recognize eight species for *Chalodeta* in the systematic checklist below. *Chalodeta theodora* is highly variable even within populations, and as the name *stilbos* Stichel 1910 does not represent a geographically discrete phenotype, it is synonymized with *C. theodora.* A dash "—" indicates a synonym.

Chalodeta Stichel 1910
chelonis group
    chaonitis (Hewitson 1866)
    chelonis (Hewitson 1866)
    chitinosa Hall, n. sp.
    chlosine Hall, n. sp.
theodora group
    lypera (Bates 1868)
    —*speusippa* Schaus 1928
    panurga Stichel 1910
    pescada Hall and Willmott 1998
    theodora (C. and R. Felder 1862)
    —*stilbos* Stichel 1910, **n. syn.**
    —*calligramma* (Rebillard 1958)

KEY TO SPECIES OF *CHALODETA* (MALES)

No key is given for females as those of *C. chlosine, C. pescada* and *C. panurga* are not known.

1. Dorsal submargin with one silverish colored line 2
– Dorsal submargin with two silverish colored lines 4
2(1). Ventral surface prominently iridescent blue 3
– Ventral surface brown with faint purple iridescence . . . . *lypera*
3(2). Dorsal surface with dark shades of iridescent blue . . . . *panurga*
– Dorsal surface brown . . . . *pescada*
4(1). Dorsal submarginal lines closely spaced, narrow and bluish silver 5
– Dorsal submarginal lines distantly spaced, broad and greenish silver . . . . *theodora*
5(4). Dorsal postdiscal line with no dark shading proximally 6
– Dorsal postdiscal line with dark shading proximally 7
6(5). Forewing length typically 16 mm, forewing apex strongly falcate, ventral purple iridescence strong . . . . *chelonis*
– Forewing length typically 13 mm, forewing apex weakly falcate, ventral purple iridescence weak . . . . *chlosine*
7(5). Dark shading proximal to dorsal postdiscal line narrow, distal portion of dorsal wings brown . . . . *chitinosa*
– Dark shading proximal to dorsal postdiscal line broad, distal portion of dorsal wings greenish brown . . . . *chaonitis*

Biogeography.—*Chalodeta* species are distributed throughout the Neotropics, from Mexico to west Ecuador, throughout the Amazon basin and Guianas, and extend as far as southeastern Brazil (see Fig. 5). Two species, *C. panurga* and *C. pescada* exclusively inhabit lower premontane forest (Hall and Willmott 1998), while the remainder inhabit wet lowland rainforest and may also extend into lower premontane habitats (e.g., *C. lypera, C. theodora* and *C. chelonis*). The highest number of species occurs in the five northern and central Andean countries, where all species but *C.*

chelonis, a southeastern Brazilian endemic, should occur. Only *C. lypera* and *C. chaonitis* are known to occur west of the Andes and throughout the Guianas.

Biology.—All *Chalodeta* species except *C. theodora* are uncommon to very rare. Males are rarely encountered perching in small groups on hilltops, along streamsides or shaded forest paths at a variety of heights above the ground and usually in the early morning or early to late afternoon; they make rapid sorties and rest only briefly on the tops of leaves with their wings half open (Brévignon and Gallard 1998, Hall and Willmott, unpubl. data). Males are most frequently encountered in rotting fish baited canopy and subcanopy traps (Hall and Willmott 2000), suggesting that males are infrequently seen because they perch in the canopy. Two species, *C. lypera* and *C. chaonitis* have been recorded visiting flowers (Brévignon and Gallard 1998, Hall and Willmott 2000). The early stages are known for two species, *C. lypera* (incorrectly referred to as *C. chelonis* by Kaye 1921) and *C. chaonitis,* which have been recorded feeding on young leaves and flowers of plants in the Melastomataceae, Passifloraceae and Sterculiaceae (Kaye 1921, Kirkpatrick 1954, DeVries et al. 1994). The larvae bear long tufts of lateral setae and the pupae are squat and bulbous with a broad cremaster (DeVries 1997).

REVISION OF *CHALODETA CHELONIS* GROUP

Chalodeta chelonis (Hewitson 1866)
(Figs. 1A, B; 2A; 4A; 5)

Charis chelonis Hewitson 1866: pl. 57, fig. 9. TL: Rio de Janeiro, S.E. Brazil. Syntype ♂ BMNH [examined].

Identification and taxonomy.—Typical forewing length: male 16 mm; female 15 mm. This species is readily distinguished by its large size, pointed wing shape, prominently falcate forewing apex and more uniformly pale iridescent purple ventral surface with weakly defined markings. The lack of dark shading proximal to the dorsal postdiscal bands occurs elsewhere only in *C. chlosine* (described below), which also has very similar male genitalia and appears to be its closest relative. The two species are distinguished in that species account.

Biology.—Unknown.

Distribution.—This species appears to be endemic to the northern states of southeastern Brazil.

Material examined.—BRAZIL: *Espírito Santo,* No specific locality 1 ♂, 1 ♀ BMNH; *Minas Gerais,* Campo Belo 3 ♀ ZMHU; Maromba 2 ♂ BMNH; 1 ♂ SMF; Leopoldina 1 ♂, 1 ♀ ZMHU; 1 ♂, 1 ♀ SMTD; *Rio de Janeiro,* Rio de Janeiro 1 ♂, 1 ♀ BMNH; 1 ♂ SMTD; 1 ♀ SMF; Nova Friburgo 1 ♂ BMNH; Laguna de Sacuarema 2 ♂, 1 ♀ BMNH; Petrópolis 3 ♂*, 1 ♀* USNM; Itatiaia 6 ♂, 3 ♀ SMF; No locality data 1 ♂ ZMHU. No locality data 3 ♂, 1 ♀ BMNH; 1 ♀ ZMHU; 1 ♀ SMF.

Chalodeta chlosine **Hall, new species**
(Figs. 1C, D; 2B; 5)

Description.—Male: Forewing length 13 mm. Forewing costal margin approximately straight, distal margin slightly convex; hindwing rounded. *Dorsal surface:* Forewing ground color brown with subtle greenish iridescence at oblique angle; three black marks in discal cell, one at base of cell Cu1, two towards base of cell Cu2; a disjointed black postdiscal band extends from vein 2A to costa and is proximally kinked in cell Cu1 and distally kinked in cell R4+5; two parallel submarginal silver lines encompass area of dark orange-brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2, dark orange-brown at distal margin; fringe brown with white scaling at distal tips of veins Cu2 to R4+5. Hindwing same as forewing except postdiscal band proximally kinked in cells Cu1 and M3, and fringe entirely white. *Ventral surface:* Differs from dorsal surface in following ways: Ground color pale gray brown overlaid with purple iridescence, distal margins gray without iridescence and

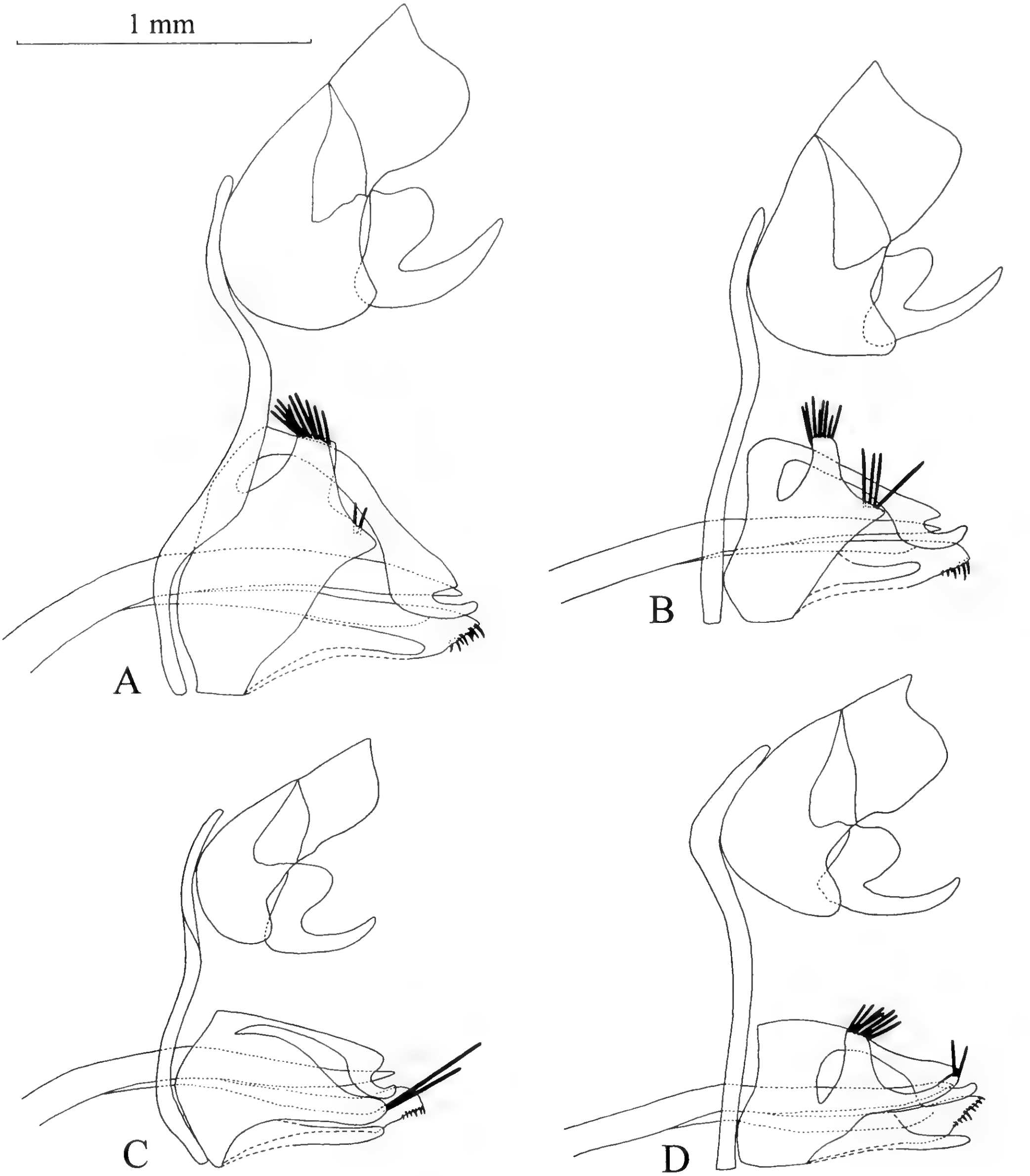

Fig. 2. Male genitalia in lateral view. A, *Chalodeta chelonis*. B, *C. chlosine*. C, *C. chitinosa*. D, *C. chaonitis*.

with undulating proximal margin, silver submarginal lines absent.

Head: Labial palpus brown. Eye brown and densely setose with brown scaling at margins. Frons brown. Antennal segments black with white scaling at base; club black, tip orange brown.

Body: Dorsal surface of thorax and abdomen dark brown, ventral surface pale brown; tegula brown. Legs brown with some iridescent purple setae.

Genitalia (Fig. 2B): Uncus rectangular, posterior dorsal margin produced into two small points medially; falces of average size and shape for family, small, deep semicircular notch in anterior margin of tegumen; vinculum narrow and ribbon-like, extends dorsally over anterior portion of tegumen;

aedeagus relatively short, narrow and straight with pointed tip; pedicel extends from a point on aedeagus one-third distance from base to tip as narrow weakly sclerotized tube to form short posterior projection tipped with a heavily sclerotized oval plate with short spines around ventral perimeter, ventrally unsclerotized except at tip; valvae consist of a short, rounded lower process that is unsclerotized at its base and an upper process with dense patches of long spines apically and on a small posteriorly projecting section medially, posteriorly elongate transtilla connected to dorsal anterior portion of upper valvae process and forms two small, upwardly curving rounded posterior projections at tip.

Female: Unknown.

Type material.—Holotype: ♂*, PERU: *Madre de Dios,* Parque Nacional Pakitza, 11°55′48″S 71°15′18″W, 340 m, 30 Sept 1991 (O. Mielke) (USNM).

Paratypes: COLOMBIA: *Putumayo,* 1 ♂: Río Mulato, Mocoa, 29 Mar 1929 (ZMHU). *Amazonas,* 1 ♂: Florida, Sept 1931 (G. Klug) (BMNH). ECUADOR: *Napo,* 1 ♂*: Tena, 1°01′S 77°49′W, 550 m, 6–10 Nov 1988 (R. Robbins) (USNM). 1 ♂*: Apuya, km 20 Tena-Puyo rd., 600 m, 6 Dec 1996 (K. Willmott) (JHKW). PERU: *Loreto,* 1 ♂: Río Pacaya, Lower Río Ucayali, Aug 1912 (BMNH). *Junín,* 1 ♂: Chanchamayo (ZSM). *Madre de Dios,* Parque Nacional Pakitza, 11°55′48″S 71°15′18″W, 340 m (USNM), 1 ♂: 14 Oct 1991 (R. Robbins), 1 ♂: 15 Oct 1991 (G. Lamas), 1 ♂*: 20 Oct 1991 (M. Casagrande). 1 ♂: Boca Río La Torre, 20 Oct 1983 (G. Lamas) (MUSM). *Puno,* 2 ♂: Yahuarmayo, 1,200 ft, Feb/Mar 1912 (H. & C. Watkins) (BMNH). BOLIVIA: *La Paz,* 1 ♂: Mapiri (SMTD). BRAZIL: *Mato Grosso,* 1 ♂*: Diamantino, Alto Rio Arinos, 14°13′S 56°12′W, 24 Sept 1989 (E. Furtado) (USNM). 3 ♂: Cuiabá (BMNH). 1 ♂: "Mato Grosso" (Zobrys & Wolter) (BMNH).

Etymology.—The species name is a euphonious anagram of "chelonis," the name of its most closely related species.

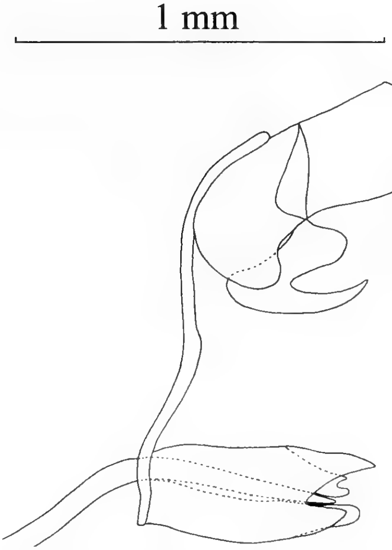

Fig. 3. Male genitalia in lateral view of *Chalodeta theodora.*

Diagnosis.—*Chalodeta chlosine* is superficially most similar to *C. chaontits* and *C. chitinosa* (described below), but lacks dark shading proximal to the dorsal postdiscal bands and has different genitalia (see those species accounts for further details). It appears to be most closely related to the southeastern Brazilian endemic *C. chelonis,* but is smaller, has a more rounded wing shape, a less falcate forewing apex, and more prominent ventral markings. The male genitalia do not differ consistently.

Biology.—*Chalodeta chlosine* is the rarest of the Amazonian *chelonis* group species. The ratio of *chlosine, chitinosa,* and *chaonitis* specimens examined in collections, respectively, is 2:7:10. An Ecuadorian male was attracted to a canopy trap baited with rotting fish.

Distribution.—This species is currently known only from the western Amazon, from Ecuador to Bolivia and into southwestern Brazil.

Chalodeta chitinosa Hall, new species

(Figs. 1E, F; 2C; 4B; 5)

Description.—Male: Forewing length 14 mm. Forewing costal margin approximately

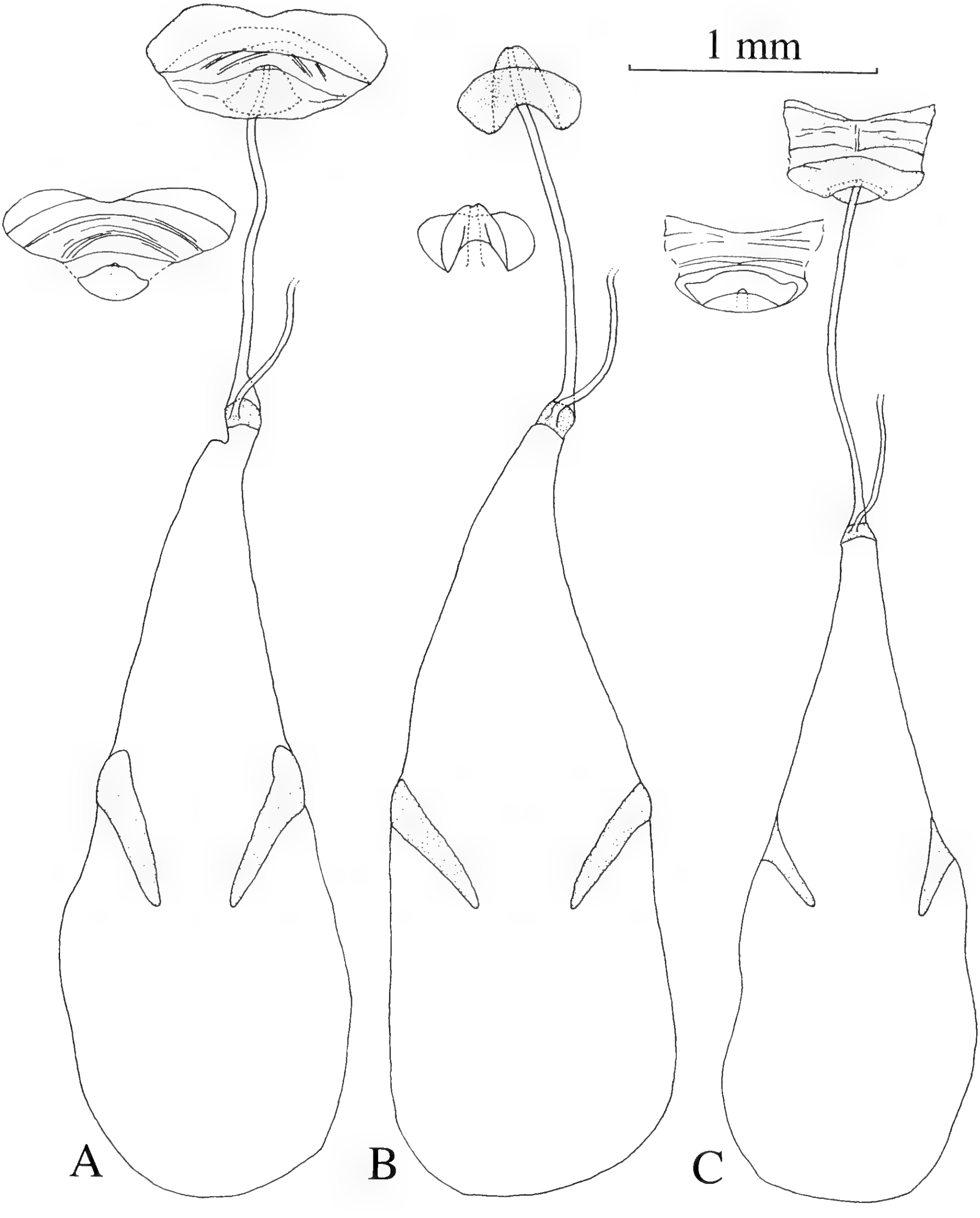

Fig. 4. Female genitalia. A, *Chalodeta chelonis.* B, *C. chitinosa.* C, *C. chaonitis.*

straight, distal margin slightly convex; hindwing rounded. *Dorsal surface:* Forewing ground color brown with subtle greenish iridescence at oblique angle; three black marks in discal cell, one at base of cell Cu1, two towards base of cell Cu2; a disjointed black postdiscal band extends from vein 2A to costa and is proximally kinked in cells Cu1 and M3, black scaling extends proximally; two parallel submarginal silver lines encompass area of dark orange brown scaling containing a single black spot in each of cells Cu1 to R4+5 and two in cell Cu2, dark orange brown at distal margin; fringe brown with white scaling at distal tips of veins Cu2 to R4+5. Hindwing same as forewing except black scaling proximal to postdiscal band considerably less prominent. *Ventral surface:* differs from dorsal surface as follows: ground color pale gray brown overlaid with purple iridescence, distal margins gray without iridescence (especially hindwing) and with undulating proximal margin, silver submarginal lines absent.

Head: Labial palpus brown. Eye brown and densely setose with brown scaling at margins. Frons brown. Antennal segments black with white scaling at base; club black, tip orange brown.

Body: Dorsal surface of thorax and abdomen dark brown, ventral surface pale brown; tegula brown. Legs brown with some iridescent purple setae.

Genitalia (Fig. 2C): Uncus rectangular, posterior dorsal margin approximately straight; falces of average size and shape for family, small, deep semicircular notch in anterior margin of tegumen; vinculum narrow and ribbon-like, extends dorsally over anterior portion of tegumen; aedeagus relatively short, narrow and straight with pointed tip; pedicel extends from a point on aedeagus one-third distance from base to tip as narrow weakly sclerotized tube to form short posterior projection tipped with a heavily sclerotized oval plate with short spines around ventral perimeter, ventrally unsclerotized except at tip; valvae consist of a short, rounded lower process that is unsclerotized at its base and a tapering, rounded posteriorly projecting upper process with two long stout spines at tip, posteriorly elongate transtilla connected to dorsal anterior portion of upper valvae process and forms two small, upwardly curving rounded posterior projections at tip.

Female: Differs from male as follows: Distal margin of forewing more convex. *Dorsal surface:* Ground color paler. *Ventral surface:* Ground color brown with no purple iridescence, distal margins and wing bases pale orange brown.

Genitalia (Fig. 4B): Corpus bursae elongate, signa medium-sized spine-like invaginations; ductus bursae narrow and membranous with small sclerotized ventral plate at anterior end, ductus seminalis connects to this sclerotized plate; eighth abdominal sternite a small sclerotized plate with medially and ventrally positioned ostium bursae forming a rounded posteriorly elongate projection, small round opening for ductus bursae at dorsal tip.

Type material.—Holotype: ♂*, PERU: *Huánuco,* Tingo Maria, 800 m, 24 June 1982 (S. Nicolay) (USNM).

Allotype: ♀, PERU: *Madre de Dios,* Parque Nacional Pakitza, 11°55′48″S 71°15′18″W, 340 m, 16 Sept 1989 (R. Robbins) (USNM).

Paratypes: VENEZUELA: *Amazonas,* 1 ♀: Yavita (Lichy) (AME). COLOMBIA: 1 ♂: "Caquetá," 11 Feb (ZMHU). ECUADOR: *Sucumbíos,* Limoncocha (B. Drummond) (BD), 1 ♂*: 25 Apr 1974, 1 ♀: 8 Oct 1974. PERU: *Loreto,* 1 ♀: Castaña, 0°48′22″S 75°14′40″W, 150 m, 17 Oct 1991 (G. Lamas) (USNM). 1 ♂: Puerto Almendra, Río Nanay, 03°50′S 73°23′W, 120 m, 3 Sept 1995 (R. Robbins) (USNM). Iquitos, 1 ♂: (H. Whitely) (BMNH), 1 ♂: (Hahnel) (ZMHU). 1 ♂: Pebas (Hahnel) (ZMHU). *San Martín,* Yurimaguas, 1898 (Michael) (ZMHU). 1 ♂: Juanjui (RPM). *Pasco,* 1 ♀: Monte Alegro, Río Pachitea (G. Tessman) (ZMHU). 1 ♂: Pachitea (SMTD). *Madre de Dios,* Parque Nacional Pakitza, 11°55′48″S 71°15′18″W, 340 m (USNM), 2 ♂: 23 Sept 1989 (D. Harvey), 1 ♂: 27 Sept 1991 (O. Mielke), 2 ♀: 2 Oct 1991 (G. Lamas), 1 ♂: 6 Oct 1990 (R. Robbins), 1 ♂, 1 ♀*: 6 Oct 1991 (R. Robbins), 1 ♂: 10 Oct 1991 (O. Mielke), 1 ♂: 11 Oct 1991 (R. Robbins), 1 ♂: 12 Oct 1991 (O. Mielke), 2 ♂: 15 Oct 1991 (O Mielke), 1 ♂*: 17 Oct 1991 (O. Mielke), 1 ♂: 20 Oct 1991 (O. Mielke). 1 ♂: 30 km S.W. of Puerto Maldonado, 300 m, 22 Oct 1983 (S. Nicolay) (USNM). 1 ♂: "Peru" (SMF). *Puno,* 1F: La Union, Río Huacamayo & Río Carabaya, 2,000 ft, Nov 1904 (Ockenden) (BMNH). BOLIVIA: *La*

Paz, 2 ♂: Mapiri (BMNH). 1 ♂, 1 ♀: Yungas (ZMHU). 1 ♂*: "Peru" [= Bolivia] (coll. W. Schaus) (USNM). 2 ♂: "Bolivia" (SMF). BRAZIL: *Amazonas*, São Paulo de Olivença, 6 ♂: Jan 1933 (S. Waehner) (BMNH), 1 ♀: (M. Moss) (BMNH), 1 ♀: (H. Bates) (BMNH), 2 ♂: Nov 1930 (S. Wucherpfennig) (SMF), 1 ♂: (Hahnel) (ZMHU), 3 ♂: (SMTD). 1 ♂: Tonantins (H. Bates) (BMNH). Manicoré, 1 ♂: 1887 (Hahnel) (ZMHU), 1 ♂: (SMTD). 1 ♀: Manaus, 1886 (Hahnel) (ZMHU). *Rondônia*, vicinity of Cacaulândia, 10°32′S 62°48′W, 160–350 m (J. Kemner) (USNM), 1 ♂*: 23 Oct 1991, 1 ♀: 29 Oct 1991. *Pará*, 1 ♀: km 1,666 Cuiabá-Santarém highway (C. Callaghan) (AME). 1 ♀: Itaituba, Rio Tapajós, 1890 (Michael) (ZMHU). Belém, 2 ♀: (H. Bates) (BMNH), 1 ♂: (ZMHU), 1 ♀ (ZSM). "Amazon", 1 ♂: (H. Bates) (BMNH), 1 ♂, 1 ♀: (ZSM). GUYANA: 1 ♀: "Guyana" (Parish) (BMNH).

Etymology.—The species name is a euphonious anagram of "chaonitis," the name of a closely related species.

Diagnosis.—*Chalodeta chitinosa* has long been confused with and is most similar to *C. chaonitis* and *C. chlosine*. It has some dark shading proximal to the dorsal postdiscal bands, unlike *C. chlosine*, although this is less extensive than in *C. chaonitis*, lacks the greenish-brown distal coloration of *C. chaonitis* and typically has prominent alternating white and brown hindwing fringe elements. In *C. chlosine*, the hindwing fringe is always entirely white and in *C. chaonitis* it is pale brown with only faint dirty white fringe elements. Each of these three species has a slightly different configuration to the postdiscal forewing band. In *C. chitinosa* and *C. chlosine*, the postdiscal markings in cells Cu1 and Cu2 form an outwardly directed semicircle while in *C. chaonitis* they form a stepped outwardly directed line. The postdiscal forewing spot in cell R4+5 is also more distally positioned in *C. chlosine* than it is in *C. chaonitis* and *C. chitinosa*.

The genitalia of *C. chitinosa* are the most distinctive of all species in the group. The male genitalia have a straight instead of bifid posterior dorsal margin to the uncus, a broad posteriorly tapering upper valve process that has only two long spines at the tip and lacks a second spine-tipped dorsally elongate anterior process. The female genitalia have a smaller eighth abdominal sternite that forms a single smoother sclerotized plate with a more posteriorly elongate ostium bursae.

Biology.—Unknown.

Distribution.—*Chalodeta chitinosa* occurs from Venezuela to Bolivia and throughout Amazonian Brazil. It is unclear how widely it may be distributed in the Guianas, and only a single female in the BMNH is labeled from Guyana.

Chalodeta chaonitis (Hewitson 1866)
(Figs. 1G, H; 2D; 4C; 5)

Charis chaonitis Hewitson 1866: pl. 57, figs. 7, 8. TL: "Amazon." Lectotype male BMNH [designated].

Identification and taxonomy.—Typical forewing length: both sexes 13 mm. *Chalodeta chaonitis* appears to have been described from two males and one female, all of which reside in the BMNH and bear Hewitson "Amazon" labels. However, although the two male syntypes represent *C. chaonitis* as treated here, the female syntype represents *C. chitinosa* described above. Thus, the only labeled syntype male of *C. chaonitis* in the BMNH is designated as a lectotype. It bears the following labels: "Hewitson Coll./79-69./Charis/chaonitis. 1/ Amazon." and "Type." This lectotype is designated to fix and stabilize the identity of this species.

Chalodeta chaonitis differs from *C. chitinosa* and *C. chlosine*, which have previously been confused with it, by possessing distal greenish-brown dorsal coloration, extensive dark shading proximal to the dorsal postdiscal bands, an outwardly diagonal instead of semicircular portion to the forewing postdiscal band in cells Cu1 and Cu2,

Fig. 5. Distributions of *Chalodeta chelonis* group species.

and a pale brown hindwing fringe with only weak dirty white elements. The upper valve process of the male genitalia possesses an elongate and upwardly curving posterior portion tipped with spines, and the eighth abdominal sternite of the female genitalia is divided into a heavily ribbed upper portion with the ostium bursae forming a separated ventral portion (unlike in *C. chitinosa*).

Biology.—DeVries (1997) reported finding aggregations of males perching in Ecuador along forest edges and in forest light gaps from 0.5 to 1 m above the ground between 1500 and 1530 hrs, however, these individuals may also be referrable to *C. chlosine* and *C. chitinosa. Bona fide* Ecuadorian males of *C. chaonitis* have been encountered feeding on low weedy Asteraceous flowers in secondary growth and attracted to canopy traps baited with rotting carrion in primary forest during the late afternoon (Hall and Willmott 2000). DeVries (1997) illustrated a mature larva and pupa of *C. chaonitis* reared from La Selva, Costa Rica. The larvae feed on flowers of *Miconia longifolia* (Melastomataceae) (DeVries et al. 1994).

Distribution.—This is the most widespread *chelonis* group species and ranges from Mexico to western Ecuador, the

Guianas, Amazon basin and Trinidad, and as far south as southern Brazil. The following additional localities are listed by de la Maza and de la Maza (1993) for MEXICO: *Chiapas,* No specific locality; by DeVries (1997) for COSTA RICA: *Heredia,* La Selva; *Puntarenas,* Palmar Norte; and by Barcant (1970) for TRINIDAD: Fondes Amandes. Since the report of this species in southern Mexico by de la Maza and de la Maza (1993) is not accompanied by an illustration, this record requires confirmation.

Material examined.—COSTA RICA: *Limón,* Guapiles 2 ♂ USNM. PANAMA: *Chiriquí,* No specific locality 1 ♀ BMNH; 1 ♀ ZMHU; *Canal Zone,* Cocoli 2 ♂, 1 ♀* USNM; *Darién,* Caña 2 ♂* USNM. VENEZUELA: *Bolívar,* La Vuelta, Río Caura 1 ♀ BMNH. COLOMBIA: *Huila,* Neiva 1 ♀ RPM (possibly mislabelled). ECUADOR: *El Oro,* nr. Pasaje 1 ♂ JHKW; *Sucumbíos,* Limoncocha 1 ♂ BD; *Napo,* Pano 1 ♂* JHKW; *Pastaza,* Sarayacu 1 ♂ ZMHU; *Morona-Santiago,* Bomboiza 1 ♂ JHKW; *Zamora-Chinchipe,* "Loja" 1 ♂ RPM; No locality data 1 ♂ BMNH. PERU: *Loreto,* Arcadia 2 ♂ USNM; Iquitos 1 ♂ BMNH; 1 ♂ SMTD; Pebas 1 ♂ ZMHU; *San Martín,* Río Chambirayacu, nr. Yurimaguas 1 ♂ BMNH; Juanjui 4 ♂ SMF; 1 ♂ RPM; Jepelacio 1 ♂ RPM; *Junín,* La Merced 1 ♂ BMNH; *Madre de Dios,* 10 km N. of Puerto Maldonado 1 ♂ USNM; 30 km S.W. of Puerto Maldonado 2 ♂ USNM; *Cuzco,* No specific locality 1 ♂ ZMHU. BOLIVIA: *La Paz,* Río Songo 3 ♂ BMNH; 3 ♂ ZMHU; 1 ♂ SMTD; Río Suapi 1 ♂ BMNH; Farinas 1 ♂ BMNH; Mapiri 1 ♂ ZSM; Yungas 3 ♂ BMNH; No specific locality 2 ♂ BMNH; No locality data 1 ♂ BMNH; 1 ♂ ZMHU; 1 ♂ ZSM; 1 ♂ SMF. BRAZIL: *Amazonas,* São Paulo de Olivença 5 ♂ BMNH; 1 ♂ ZMHU; 1 ♂ SMTD; 8 ♂ SMF; Río Tacana 1 ♂ SMTD; Fonteboa 1 ♂ BMNH; Tefé 3 ♂ BMNH; Manicoré 1 ♂ SMF; Parintins 1 ♂ BMNH; Upper Amazon 1 ♂ ZMHU; 3 ♂ BMNH; 1 ♂ SMTD; *Pará,* Belém 1 ♂ ZMHU; *Mato Grosso,* Cuiabá 4 ♂ BMNH; Melguira, 10 km S. of Diamantino 1 ♂ BMNH; No specific locality 1 ♂ ZMHU; *Distrito Federal,* Planaltina 1 ♂ USNM; Parque do Gama 1 ♂*, 1F USNM; *Goiás,* Vianópolis 1 ♂ SMF. GUYANA: No locality data 1 ♀ BMNH. SURINAM: No locality data 1 ♂ ZMHU. FRENCH GUIANA: *Saint Laurent du Maroni,* Saint Laurent du Maroni 1 ♂ BMNH; *Cayenne,* Cayenne 2 ♂ BMNH; 1 ♂ RPM; Sinnamary 1 ♂* USNM; Saint Georges 2 ♂ BMNH; No locality data 3 ♂, 1 ♀ BMNH. TRINIDAD: St. Annes 1 ♀ BMNH. No locality data 1 ♂ BMNH.

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A REVISION OF THE *ANASTREPHA SERPENTINA* SPECIES GROUP (DIPTERA: TEPHRITIDAE)

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Abstract.—The *Anastrepha serpentina* species group is revised, with a key, descriptions, illustrations, and phylogeny provided for the 11 species recognized: *A. anomala* Stone, ***anomoiae,* n. sp.**, *bistrigata* Bezzi, ***normalis,* n. sp.**, *ocresia* (Walker), *ornata* Aldrich, ***pseudanomala,* n. sp.**, ***pulchella,* n. sp.**, *pulchra* Stone, *serpentina* (Wiedemann), and *striata* Schiner. Lectotypes are designated for *Anastrepha bistrigata* Bezzi, *Dacus serpentinus* Wiedemann, *Urophora vittithorax* Macquart, and *Dictya cancellaria* Fabricius.

Key Words: *Anastrepha, serpentina, striata, ornata, bistrigata,* Tephritidae, fruit flies, taxonomy, phylogeny, identification, distribution, host plants

The *serpentina* group comprises 11 species, including two of the most significant pests within the genus *Anastrepha* and several others of lesser agricultural importance. *Anastrepha serpentina* (Wiedemann) is an especially important pest of sapotaceous fruits, such as star apple, sapotes, and nispero, and *A. striata* Schiner is among the worst pests of Myrtaceae, especially guavas, although both species also sometimes attack mango, mombins, citrus, and various other fruits (see Norrbom, in press). As delimited here, the *serpentina* group comprises four previously included species, three species formerly recognized as the *striata* group (see Norrbom et al. 1999b), and four newly described species.

The *serpentina* group is most diverse in Central America and northern South America, although *A. serpentina* and *striata* extend north to Mexico or southern Texas and *A. serpentina* extends south to Argentina, and *A. ocresia* is known only from the Antilles and southern Florida.

Host plants are known for eight of the 11 species. Although the host range for the species group is very diverse, the native hosts are mainly in three families. Two species (*A. anomala* Stone and *A. normalis,* n. sp.) have only species of Apocynaceae as known hosts, whereas *A. pulchra* Stone is known only from Sapotaceae, which also includes the main hosts of the generalist species *A. serpentina.* The only native host known for *A. ocresia* (Walker) belongs to the Myrtaceae, but it has been reared from an exotic species of Sapotaceae. The only known native host plant of *A. ornata* Aldrich, and most of those of *A. striata* and *A. bistrigata* Bezzi, belong to the family Myrtaceae.

MATERIALS AND METHODS

Terminology follows the glossary of White et al. (1999). Acronyms for institutions where specimens are deposited follow Thompson (1999). Phylogenetic analysis was conducted using Hennig86 (© J. S.

Farris) and the cladogram figures were produced using Winclada (© K. C. Nixon).

KEY TO THE SPECIES OF THE *ANASTREPHA SERPENTINA* GROUP

1. Wing with C-band and S-band well separated (Fig. 2I); middle section of S-band very narrow, distal section broad; proximal arm of V-band connected along posterior wing margin to basal extension of S-band along vein A_1+Cu_2. Thorax with darker areas mostly brown (Fig. 1D). Oviscape 3.40–3.95 mm long. Aculeus tip broadly triangular (Fig. 11A). Colombia, Ecuador . . . *A. ornata* Aldrich
- C-band and S-band connected (Figs. 2A–H, 3A–G) or at most very narrowly separated (Fig. 3H); middle section of S-band broad, or if narrow, distal section also narrow; proximal arm of V-band not connected to basal extension of S-band along posterior wing margin except sometimes in *A. pulchella*. Other characters variable 2
2. Wing cell br with hyaline area posterior to pterostigma broadly extended to vein R_{4+5} (Figs. 2D, 3F–H). Abdomen with all tergites mostly yellow to orange, without brown markings (Figs. 1A, H). Thoracic pleuron without brown areas. Epandrium with narrow, V-shaped, medial indentation in dorsal posterior margin; lateral surstylus with rounded subapical lateral lobe (Figs. 4F, 7F). Aculeus tip broadly triangular, at least 0.17 mm wide (Figs. 11A, C) 3
- Cell br entirely infuscated (Figs. 2C, 3A–C) or with hyaline area not extended to vein R_{4+5} (Figs. 2A–B, E–H, J, 3D–E). Abdomen with brown bands or spots on at least syntergite 1+2 and tergite 3, or more extensively brown (Figs. 1B–G). Thoracic pleuron usually with at least anepimeron partially brown (orange in *A. ocresia*). Epandrium with dorsal posterior margin evenly rounded or at most with slight indentation; lateral surstylus without rounded subapical lateral lobe. Aculeus tip variable in shape 4
3. Oviscape less than 2.8 mm long, less than 0.90 times mesonotum length (Fig. 1H). Aculeus less than 2.5 mm long. Scutum with brown areas usually interrupted at transverse suture; setulae usually strongly contrasting white and dark brown, absent on narrow area lateral to postsutural nonmicrotrichose area. Distal section of S-band slightly narrowed to moderately broad, at apex of vein R_{2+3} 0.44–0.63 times width of cell r_{2+3} (Figs. 3F–H). Widespread, Mexico to Bolivia and Brazil . . . . *A. striata* Schiner
- Oviscape more than 3.0 mm long, more than 0.90 times mesonotum length (Fig. 1A). Aculeus more than 3.0 mm long. Scutum with brown area narrowed but uninterrupted at transverse suture; setulae yellow and brown, less dense but more or less continuous lateral to postsutural nonmicrotrichose area. Distal section of S-band slender, at apex of vein R_{2+3} 0.36–0.44 times width of cell r_{2+3} (Fig. 2D). Southern Brazil . . . . *A. bistrigata* Bezzi
4. Wing with C-band and S-band very broadly connected basally, cell br without hyaline area in apical half (Figs. 2C, 3A–C); C-band with yellow area posterior to pterostigma small, not extending beyond cell r_1 or level of basal third of pterostigma; ratio of length of section of vein M between crossveins R-M and DM-Cu: length of DM-Cu 0.48–0.69; distal section of S-band slender, its width at apex of vein R_{2+3} less than 0.45 width of cell r_{2+3} . . 5
- C-band and S-band less broadly connected, cell br with at least a small hyaline area in apical half (Figs. 2A–B, E–H, J, 3D–E); C-band with yellow area posterior to pterostigma large, extending into cells r_1 and r_{2+3} at least to level of midlength of pterostigma; ratio of length of section of vein M between crossveins R-M and DM-Cu: length of DM-Cu 0.68–0.91; distal section of S-band variable in width 7
5. Wing with proximal arm of V-band with anterior end more proximal than posterior end and connected to S-band near middle of crossvein R-M (Fig. 2C); posterior end not extended basally along posterior wing margin. Aculeus 3.66 mm long; tip 0.86 mm long, serrate only on apex (Figs. 9B, 10D). Panama, Colombia . . . . . . *A. anomoiae* Norrbom, n. sp.
- Proximal arm of V-band with anterior end at least slightly more distal than posterior end, and separated from S-band or connected along vein R_{4+5} (Figs. 3A–C); posterior end extended basally along posterior wing margin. Aculeus 4.00–5.70 mm long; tip less than 0.50 mm long, nonserrate or more than half serrate (Figs. 10I–J) 6
6. Wing cell r_1 with hyaline spot between S-band and vein R_{2+3} (Fig. 3A); apex of proximal marginal hyaline spot in cell r_1 aligned proximal to crossvein R-M. Orbital plate yellow (Fig. 1E). Aculeus tip 0.24–0.26 mm long, more than half serrate (Fig. 10I). Panama . . . . *A. pulchella* Norrbom, n. sp.
- Cell r_1 without hyaline spot between S-band and vein R_{2+3} (Figs. 3B–C); apex of marginal hyaline spot in cell r_1 aligned with or distal to crossvein R-M. Orbital plate with triangular brown mark (Fig. 1F). Aculeus tip 0.33–

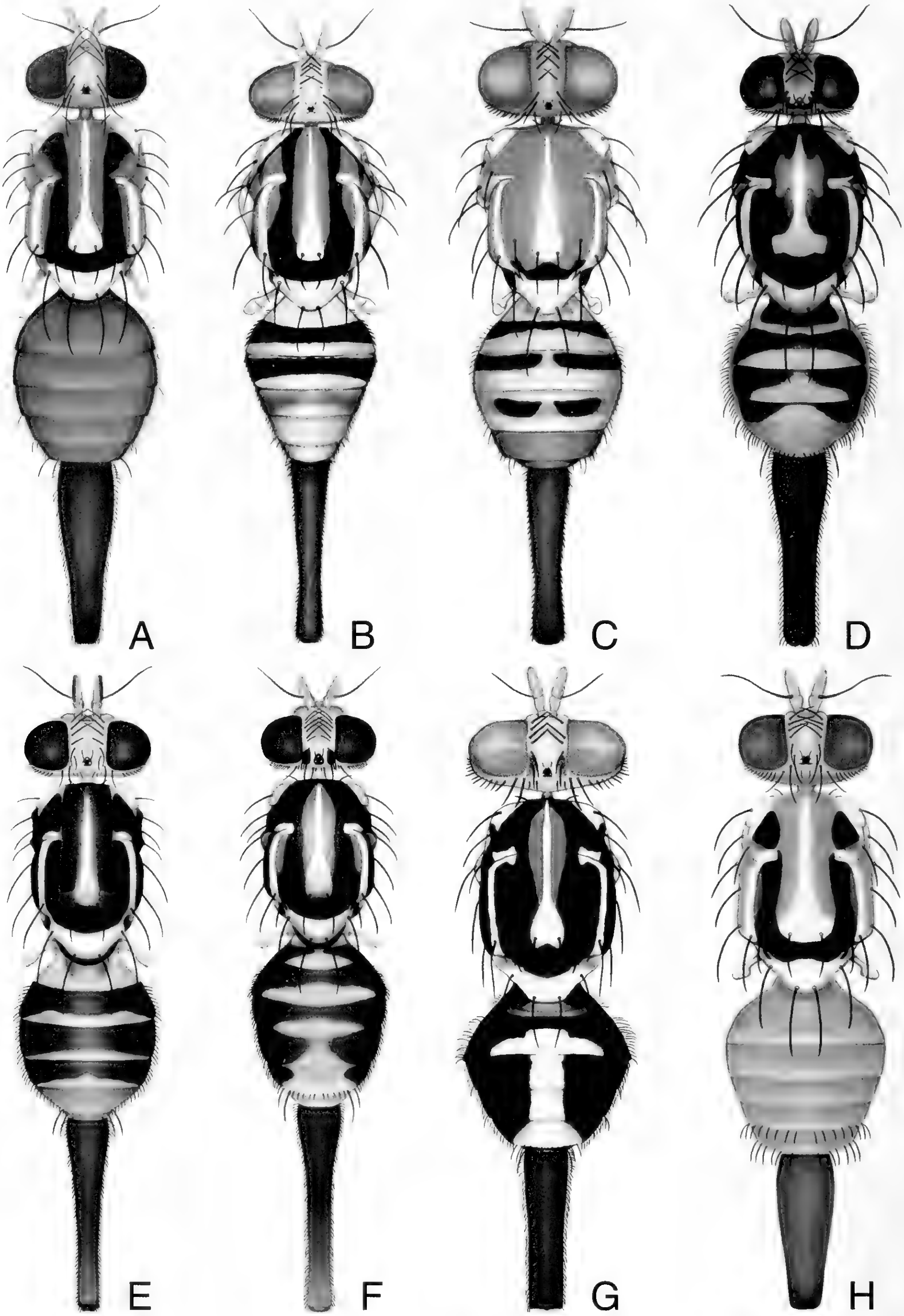

Fig. 1. Dorsal habitus. A, *Anastrepha bistrigata* (USNM53046, Brazil: ex. USP lab colony). B, *A. normalis* (USNM47450, Venezuela). C, *A. ocresia* (USNM51938, Dominican Republic: 2 km N Bayahibe). D, *A. ornata* (USNM51868, Colombia: El Retiro). E, *A. pulchella* (USNM52982, Panama: Barro Colorado I.). F, *A. pulchra* (USNM00052975, Panama: La Campana). G, *A. serpentina* (USNM47625, Venezuela: Pueblo Nuevo). H, *A. striata* (USNM51843, Costa Rica: Jardin Las Cruces).

0.46 mm long, nonserrate (Fig. 10J). Panama, Venezuela, n. Brazil . . . . *A. pulchra* Stone

7. Mesonotum with brown areas extensive, extending to or nearly to anterior margin of scutum (Figs. 1B, E–G). Scutum microtrichose except presutural medial bare area. Wing with distal section of S-band slender to moderately broad, at apex of vein R_{2+3} 0.32–0.64 times width of cell r_{2+3}; distal arm of V-band usually absent (except in sp. from Mexico) . . . 8

– Mesonotum with brown markings only near scuto-scutellar suture (Fig. 1C). Scutum without microtrichia except on extreme lateral margin. Wing with distal section of S-band very broad, at apex of vein R_{2+3} at least 0.73 times width of cell r_{2+3} (Fig. 2H); distal arm of V-band present from vein M to posterior wing margin. Greater Antilles, USA (southern Florida) . . . . *A. ocresia* (Walker)

8. Abdomen orange with brown bands on syntergite 1+2, tergite 3, and sometimes tergite 4 (Figs. 1B, E–F). Wing with distal section of S-band usually slightly narrowed to moderately broad, at apex of vein R_{2+3} 0.47–0.64 times width of cell r_{2+3} (Figs. 2A, E–G, J), rarely (Brazilian *anomala*) more slender (Fig. 2B). Oviscape 3.70–5.51 mm long, 1.02–1.56 times mesonotum length. Aculeus tip variable 9

– Abdomen mostly brown with T-shaped medial yellow mark (Fig. 1G). Distal section of S-band slender, at apex of vein R_{2+3} 0.32–0.43 times width of cell r_{2+3} (Figs. 3D–E). Oviscape 2.58–3.91 mm long, 0.79–1.02 times mesonotum length. Aculeus tip 0.37–0.46 mm long, 0.14–0.17 mm wide, finely serrate on more than distal half (Fig. 11B). Widespread, Mexico to Argentina . . . . *A. serpentina* (Wiedemann)

9. Wing with distal arm of V-band complete (Fig. 2E). Southern Mexico . . . . *Anastrepha* sp.

– Distal arm of V-band absent or at most consisting of small, faint spot in cell m (Figs. 2A–B, F–G, J) 10

10. Wing with middle section of S-band entirely brown anterior and distal to crossvein R-M (Figs. 2A–B, J). Oviscape 3.70–5.51 mm long, 1.02–1.56 times mesonotum length. Aculeus 3.62–5.51 mm long; tip more than 2 times as long as wide, finely serrate on distal half or more (except some Brazilian *anomala*), 0.19–0.40 mm long (Figs. 10A–C, H). Lateral surstylus sometimes with strong basolateral lobe (Figs. 4A–B) 11

– Middle section of S-band mostly orange, including anterior and distal to crossvein R-M, brown only narrowly on margins (Figs. 2F–G). Oviscape 3.79–4.41 mm long, 1.07–1.21 times mesonotum length. Aculeus 3.62–4.14 mm long; tip less than 2 times as long as wide, nonserrate, 0.23–0.28 mm long (Fig. 10F). Lateral surstylus without strong basolateral lobe (Figs. 5A–B). Panama, Venezuela . . . . *A. normalis* Norrbom, n. sp.

11. Aculeus tip 0.09–0.12 mm wide, gradually tapered (Figs. 9A, 10A–C). Oviscape 4.49–5.51 mm long, 1.44–1.56 times mesonotum length (except 3.70 mm long, 1.02 times mesonotum in Bahia, Brazil female). Aculeus usually 4.37–5.51 mm long (3.62 mm long in Bahia female). Lateral surstylus with strong basolateral lobe (Figs. 4A–B). Panama, Brazil . . . . *A. anomala* Stone

– Aculeus tip 0.15 mm wide, with nonserrate basal part nearly parallel sided (Figs. 9D, 10H). Oviscape 4.11–4.28 mm long, 1.11–1.18 times mesonotum length. Aculeus 4.16 mm long. Male unknown. Costa Rica, Panama . . . . *A. pseudanomala* Norrbom, n. sp.

Anastrepha anomala Stone
(Figs. 2A–B, 4A–B, 8A, 9A, 10A–C)

Anastrepha anomala Stone 1942: 29; Foote 1967: 7 [in catalog]; Steyskal 1977: 8 [in key]; Zucchi 1983: 280, 2000: 238 [Brazil, Bahia]; Norrbom et al. 1999a: 77 [in catalog]; Norrbom, in press [host database].

Recognition.—*Anastrepha anomala* is one of the species of the *serpentina* group with a hyaline area in cell br posterior to the pterostigma that is not extended to vein R_{4+5}. Of the other species with this character, *A. anomala* is most likely to be confused with *A. normalis* and *A. pseudanomala.* It differs from both species by its more slender, tapered aculeus tip (no more than 0.12 mm wide), and at least from *A. normalis* in having a strong basolateral lobe on the lateral surstylus (the male is unknown for *A. pseudanomala*). It further differs from *A. normalis* in having the middle section of the S-band solidly dark brown anterior and distal to crossvein R-M, and the aculeus tip finely serrate on the distal half or more (except in Maranhão, Brazil female). Most females have slightly longer terminalia (oviscape more than 1.4 times mesonotum length; aculeus more than 4.3 mm long) than in *A. normalis* and *A. pseu-*

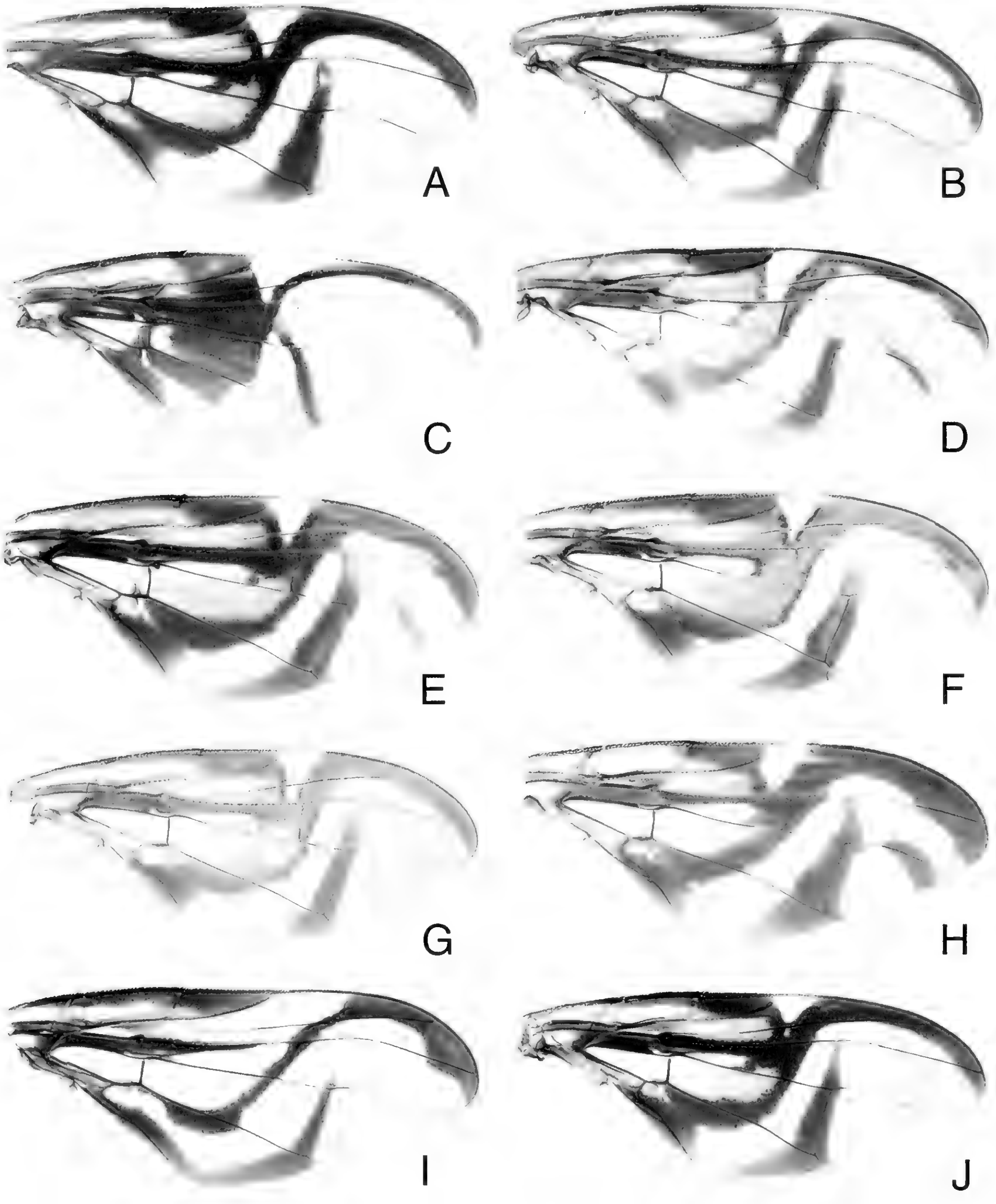

Fig. 2. Wing. A–B, *Anastrepha anomala* (USNM52954, Panama: La Campana. USNM53107, Brazil: Cruz das Almas). C, *A. anomoiae* (holotype, USNM50456, Colombia: Guaguaqui). D, *A. bistrigata* (USNM53050, Brazil: Belo Horizonte). E, *A.* sp. (USNM52942, Mexico: Tapachula). F–G, *A. normalis* (USNM52938–9, Venezuela: Marcillal de la Costa). H, *A. ocresia* (USNM51712, Cuba: Bolondron). I, *A. ornata* (holotype, USNM52985, Ecuador: Baños). J, *A. pseudanomala* (USNM50455, Costa Rica: 20 km. S Upala).

danomala, but they are shorter in a single female from Bahia, Brazil (see Comments).

Description.—Largely dark orange to dark red brown with yellow markings. Setae dark brown. *Head:* Yellow except ocellar tubercle brown. Facial carina, in profile, concave. 3–5, usually 4, frontal setae; 1–2 orbital setae, posterior seta well developed

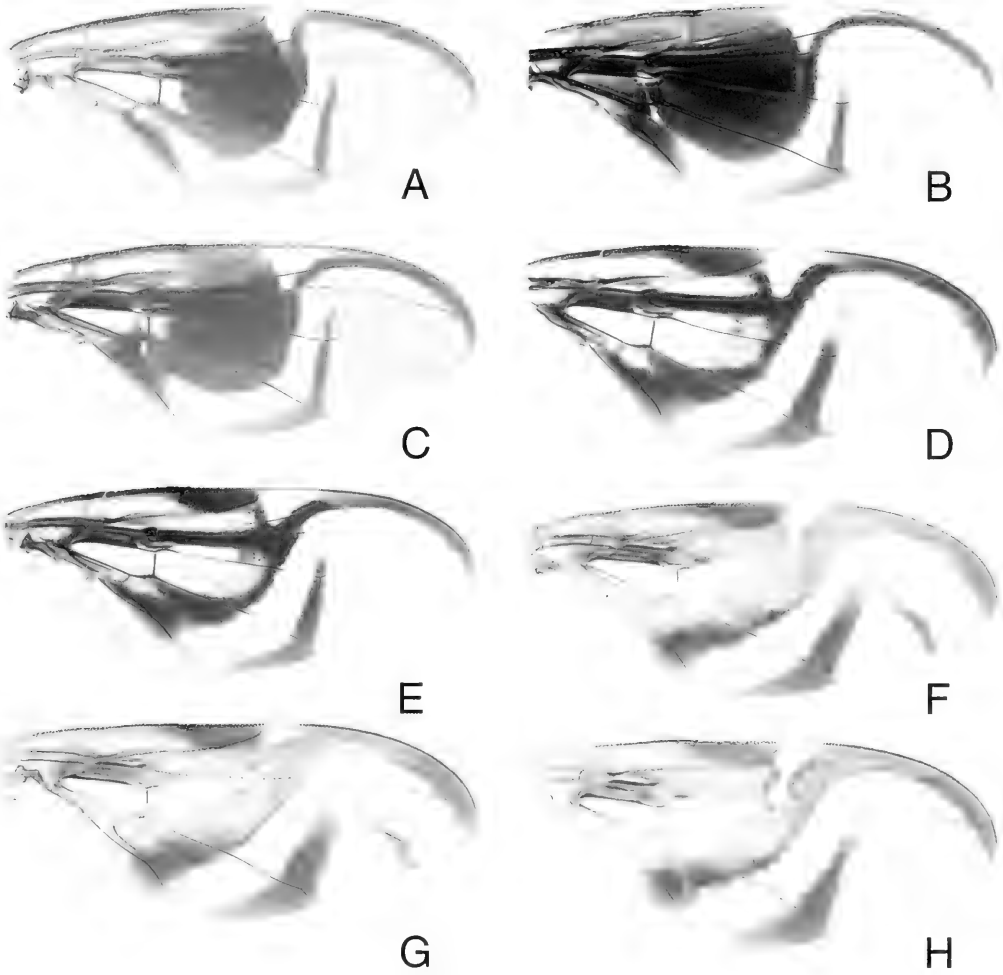

Fig. 3. Wing. A, *Anastrepha pulchella* (USNM52978, Panama: Arraijan). B–C, *A. pulchra* (Panama: El Cermeno), male (USNM51713), female (USNM51714). D–E, *A. serpentina* (USNM53098, Peru: Malambo. and USNM53097, Trinidad: nr. Teteron). F–H, *A. striata* (Colombia: Muhic. USNM53100, Trinidad: La Brea; and USNM51718, Brazil: 62 km SE Ariquemes).

if present. Ocellar seta weak, short to minute. Antenna extended 0.75–0.90 distance to lower facial margin. *Thorax:* Mostly orange to dark red brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally less than half distance from acrostichal seta to dorsocentral seta; sublateral vitta extended from transverse suture to posterior margin, including intra-alar seta; scutellum except extreme base (brown area well separated from basal seta); propleuron; dorsal margin and anteroventral corner of anepisternum; greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal pattern similar to *A. normalis* (see Fig. 1B); broad area bordering medial vitta, shorter and narrower area bordering mesal margin of sublateral vitta, and large sublateral presutural area orange. Darker areas of anepisternum and katepisternum orange; those of anepimeron, meron, and katatergite mostly dark brown. Subscutellum and mediotergite dark brown, narrowly dark orange medially. Mesonotum 3.06–3.66 mm long. Scutum microtrichose except for broad presutural bare area extended about ¾ distance to transverse suture; setulae mostly yellow, brown on parts of darker areas. Katepisternal seta weak, slightly to much shorter than postocellar seta, yellowish to red brown. *Wing* (Figs. 2A–B): Length 6.67–7.90 mm. Vein M strongly curved apically; section between BM-Cu and R-M 2.04–2.62 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.74–0.85 times as long as DM-Cu (0.69 times in Bahia female). Crossvein DM-Cu oblique, with anterior end more distal than posterior end. Pattern mostly dark brown. C-band and S-band broadly connected in cells r_{2+3} and br, but separated basally by hyaline area in posterior half of br aligned with pterostigma, hyaline basal sixth of cell dm, and hyaline to yellowish area covering all of cell bm. C-band yellowish to subhyaline in cell bc and posterior half to ⅔ of cell c; with large yellowish area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally to or almost to level of apex of vein R_1. S-band with large yellow area in cell dm usually extending into cell br and sometimes nearly touching crossvein R-M; rest of band dark brown, including areas distal to and anterior to R-M; distal section moderately broad, at apex of vein R_{2+3} 0.33–0.61 times width of cell r_{2+3} (0.49–0.61 times in Panamania specimens; 0.45 times in Maranhão, Brazil female; in Bahia female, slender at apex of R_{2+3}, 0.33–0.38 times width of cell r_{2+3}, but slightly broader along vein R_{4+5}); not extended to apex of vein M. Hyaline spot in cell r_1 nearly triangular, extended well into cell r_{2+3} and sometimes to vein R_{4+5}; its apex aligned with R-M or usually slightly basal to it. V-band with distal arm absent; proximal arm separated from S-band, extended to vein R_{4+5}; extended basally along posterior wing margin almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen:* Orange with yellow and brown markings. Syntergite 1+2 and tergites 3–4 each with band, brown laterally, orange medially, on tergite 4 often entirely orange; posterior margin yellow, narrowing laterally and on successive tergites. Tergite 5 and female tergite 6 orange. *Male terminalia* (Figs. 4A–B): Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view slightly curved; in posterior view, with strong basolateral lobe, main part narrowly triangular, acute apically. Proctiger with lateral fold separating sclerotized areas. Phallus 6.2–7.1 mm long; 1.94–2.04 times as long as mesonotum. Glans 0.50–0.55 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 4.49–5.58 mm long, 1.44–1.56 times as long as mesonotum (3.70 mm, 1.02 times mesonotum length in Bahia female). Eversible membrane (Fig. 8A) with 35–40 large, hook-like dorsobasal scales in triangular pattern. Aculeus 3.62–5.51 mm long (4.37–5.12 mm in Panamanian females; 5.51 mm in Maranhão female; 3.62 mm in Bahia female); tip (Figs. 9A, 10A–C) 0.19–0.32 mm long, 0.09–0.12 mm wide (0.27–0.32 mm long, 0.105–0.12 mm wide in Panamanian females; 0.24 mm long, 0.10 mm wide in Bahia female; 0.19 mm long, 0.09 mm wide in Maranhão female), gradually tapered, very finely serrate on apical 0.60–0.67 in Panamanian females, on apical 0.50 in Bahia female, nonserrate in Maranhão female. Spermathecae ovoid. *Egg:* Similar in shape to *A. serpentina,* posterior end elongate and tapered. Anterior end without lobe (i.e., micropyle at apex). Length 1.75–1.82 mm, broadest width 0.20–0.22 mm.

Distribution.—*Anastrepha anomala* is known with certainty only from Panama and Brazil, although the status of the Brazilian populations needs further study (see Comments). Records from Venezuela (Caraballo 1981) were based on misidentifications of *A. normalis.* The record from Guatemala (Norrbom et al. 1999a) is unconfirmed. It was based on a male (J. López,

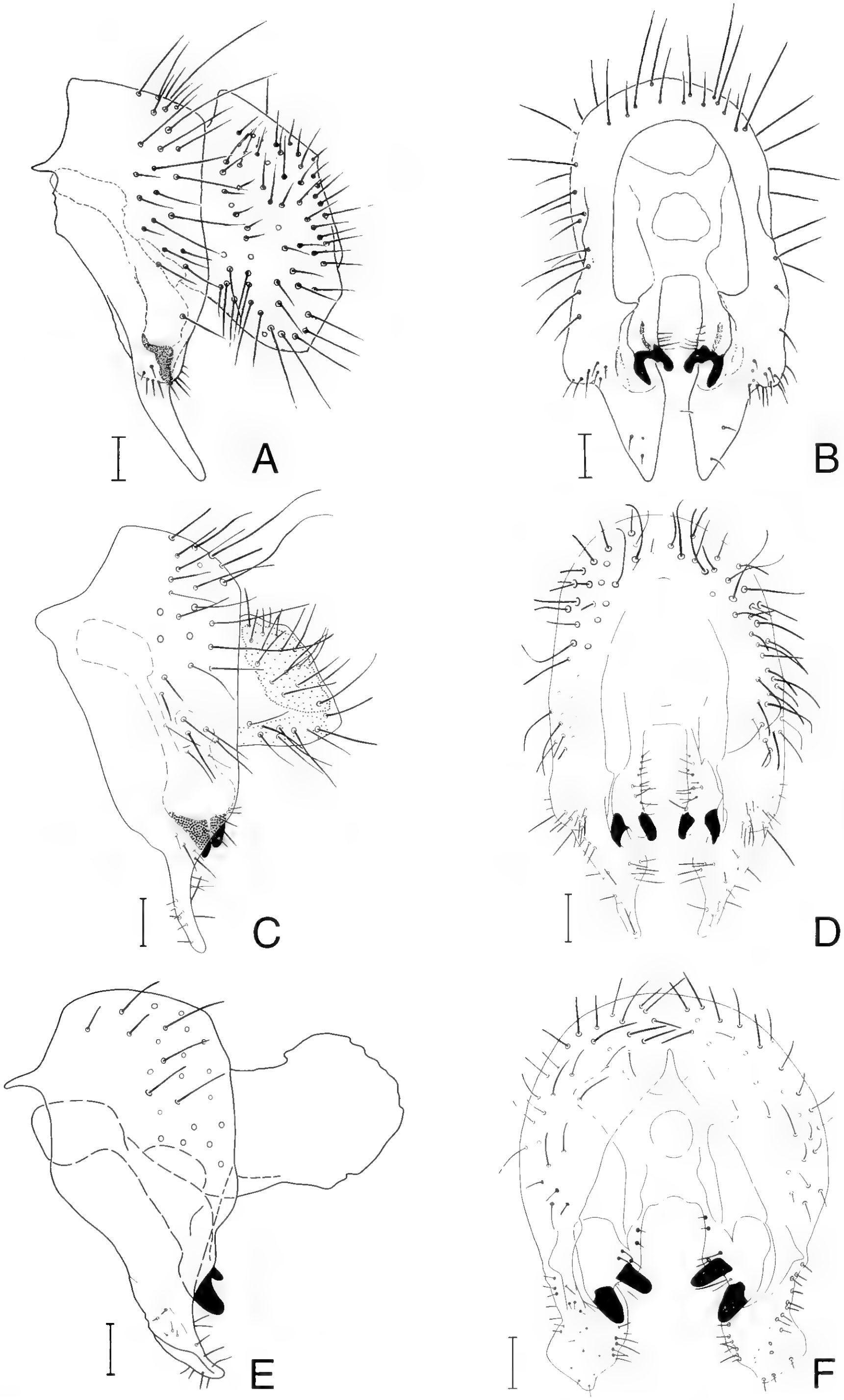

Fig. 4. Epandrium and surstyli, lateral and posterior views. A–B, *Anastrepha anomala* (USNM52956, Panama: Barro Colorado I.). C–D, *A. anomoiae* (USNM50457, Panama: El Valle). E–F, A. bistrigata (USNM53047, Brazil: Univ. of São Paulo culture).

personal communication) that might be conspecific with the undetermined male from Mexico reported here.

Biology.—The holotype and some of the paratypes were reared from seeds of *Lacmellea panamensis* (Woodson) Markgr. (Apocynaceae) (Stone 1942, as *Zschokkea panamensis*).

Comments.—The description of the egg is based on a sample of five dissected from the abdomen of the female from Arraijan, Panama (USNM52951). The aculeus tip is very finely serrate in the Panamanian specimens, but more extensively so than indicated by Stone (1942).

The status of the populations represented by single females from Bahia and Maranhão, Brazil (R. A. Zucchi, personal communication) needs further study. They may be distinct species. The Bahia female differs from specimens from Panama in having shorter terminalia (oviscape 3.70 mm long and 1.02 times mesonotum length; aculeus 3.62 mm long), a slightly shorter, blunter, and less serrate aculeus tip, and a slightly narrower distal section of the S-band (less than 0.40 times width of cell r_{2+3} at apex of vein R_{2+3}). It also has a spur vein in cell r_{4+5} anterior to crossvein DM-Cu, but this is probably an anomaly. The female from Maranhão has relatively long terminalia (oviscape 5.51 mm long and 1.56 times mesonotum length; aculeus 5.51 mm long) but the aculeus tip is short (0.19 mm) and nonserrate. The width of the distal section of its S-band is intermediate between the Panamanian and Bahian specimens.

Type data.—Holotype ♀ (USNM52966), PANAMA: Panamá: Barro Colorado Island [9°9′17N 79°50′53W], reared ex. seeds of *Zschokkea panamensis* [= *Lacmellea panamensis*], 17 Mar 1937, J. Zetek 3814 [examined].

Other specimen data.—BRAZIL: Bahia: Cruz das Almas, Fazenda Chapadinha, 14 Jun 1978, A. S. Nascimento, 1 ♀ (ESALQ, USNM53107). Maranhão: Itapecuru-Mirim, 2000, R. N. S. Lemos, 1 ♀ (ESALQ USNM31431). PANAMA: Panamá: Arraijan [8°57′N 79°39′W], 9 Jun 1949, J. Zetek 5401, 1 ♂ (USNM52950); same, 21 Sep 1950, J. Zetek 5478, 1 ♀ (USNM52951); same data as holotype except Jan 1939, J. Zetek 4329, 4 ♂, 1 ♀ paratypes (USNM52954–8), 1 ♀ paratype (TAMU USNM52959); same, 4–7 Jan 1937, J. Zetek 3777, 2 ♂ paratypes (TAMU USNM52952; BMNH USNM53115); same, 17–23 Mar 1937, J. Zetek 3814, 1 ♂ paratype (USNM52953), 1 ♂ paratype (IOC USNM53105).

Anastrepha anomoiae Norrbom, new species

(Figs. 2C, 4C–D, 8B, 9B, 10D)

Recognition.—*Anastrepha anomoiae* is one of three species of the *serpentina* group with the C- and S-bands broadly fused so that there is no hyaline area in the middle of cell br. It differs from all other known species of *Anastrepha* in having the proximal arm of the V-band strongly oblique, with the anterior end more proximal than the posterior end, and connected to the S-band near the middle of crossvein R-M. Crossvein DM-Cu, which is covered by this band, is also oblique in this direction or perpendicular to the long axis of the wing. The posterior end of the V-band does not extend basally along the posterior wing margin. The extremely long aculeus tip (0.86 mm long), which tapers slightly subbasally and is bluntly rounded distally, is also distinctive. The very slender distal section of the S-band, and the dark colors of the wing pattern and the darker areas of the body are additional useful diagnostic characters.

Description.—Largely dark orange to dark red brown with yellow markings. Setae red brown to dark brown. *Head:* Mostly yellow. Frons, face and gena orange to reddish brown in holotype (possibly discoloration). Ocellar tubercle brown. Occiput in holotype with paired small brown spot dorsally and larger spot ventrally, extending to postgena. Facial carina, in profile, concave. 4–5 frontal setae; 2 orbital setae, posterior seta well developed. Ocellar seta weak. An-

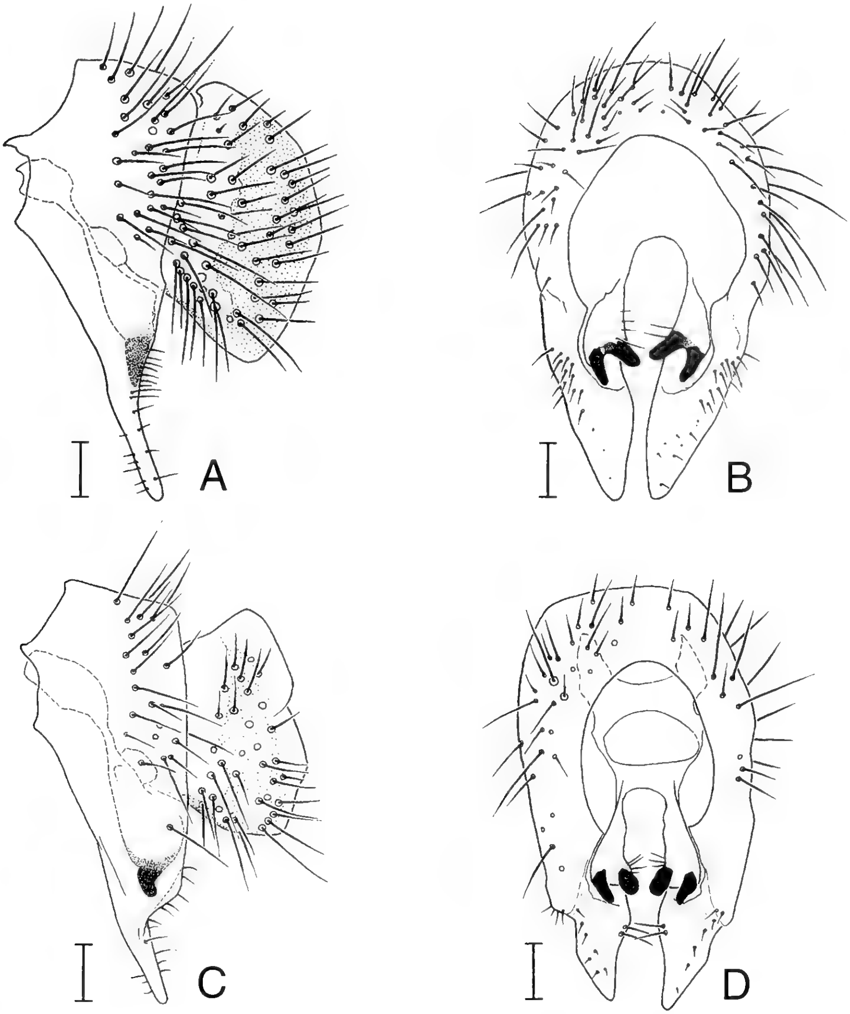

Fig. 5. Epandrium and surstyli, lateral and posterior views. A–B, *Anastrepha normalis* (USNM52938, Venezuela: Marcillal de la Costa). C–D, *A. ocresia* (USNM52992, Cuba: Guantanamo airbase).

tenna extended 0.75–0.85 distance to lower facial margin. *Thorax:* Mostly orange brown to red brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally only slightly beyond level of acrostichal seta (at most half distance to level of dorsocentral seta); sublateral vitta extended from transverse suture to or almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area well separated from basal seta); dorsal margin of anepisternum; most of greater ampulla; large dorsal spot on katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal darker areas mostly dark orange, but anterolateral corner, lateral margin of presutural area, margin along mesal side of lateral vitta, somewhat U-shaped posterior area, postsutural lateral areas, and notopleuron dark brown; without orange vitta on dorsocentral line. Darker area of anepisternum about half to entirely brown.

Anepimeron mostly dark brown. Darker areas of katepisternum, meron and katatergite dark orange or dark brown. Subscutellum and mediotergite dark orange to dark brown. Mesonotum 3.49–4.00 mm long. Scutum microtrichose except for broad medial anterior area extended ⅓–⅔ distance to transverse suture; setulae mostly brown, but yellow on medial stripe and in broad presutural area. Katepisternal seta weak, no longer than postocellar seta, yellowish to pale brown. *Wing* (Fig. 2C): Length 7.5–9.0 mm. Vein M moderately curved apically; section between BM-Cu and R-M 2.4–2.9 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.63–0.69 times as long as DM-Cu. Crossvein DM-Cu perpendicular to long axis of wing or oblique, with anterior end more proximal than posterior end. Pattern mostly dark brown. Basally with large infuscated area formed by fusion of C-band and base of S-band, which are separated only by hyaline to yellowish area covering much of cell bm; basal area mostly brown, but most of cells bc and c and part of cell bcu yellowish to subhyaline, small basal spot in cell dm and small area in cells sc and r_1 posterior to bend in vein sc yellow; cell r_{2+3} basal to R-M and all of cell br brown. Remainder of S-band brown; distal section very slender, at apex of vein R_{2+3} 0.27–0.33 times width of cell r_{2+3}; closely following vein R_{2+3} so that hyaline spot in cell r_1 is elongate along costa; not extended to apex of vein M. Hyaline spot in cell r_1 extended to vein R_{4+5}; its apex aligned with R-M. V-band with distal arm absent; proximal arm very slender, strongly oblique and connected to S-band in cell r_{4+5} near middle of crossvein R-M; not extended basally along posterior wing margin. *Abdomen:* Orange with yellow and dark brown bands. Syntergite 1+2 with medial to subapical brown band, broader in male; posterior margin yellow, narrowing laterally. Tergites 3 and 4 with broad brown band, narrowed medially; posterior margin yellow, narrowing laterally. Male tergite 5 orange. *Male terminalia* (Figs. 4C–D): Dorsal posterior margin of epandrium convex with slight medial angle. Lateral surstylus moderately long; in lateral view very slightly curved; in posterior view with moderate basolateral lobe, main part strongly tapered, slender apically. Proctiger with lateral fold separating sclerotized areas. Phallus 4.58 mm long; 1.31 times as long as mesonotum. Glans 0.65 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape of holotype damaged, but probably more than 3.7 mm long. Eversible membrane (Fig. 8B) with 60–70 large, hook-like dorsobasal scales in triangular pattern. Aculeus 3.66 mm long; base expanded; tip (Figs. 9B, 10D) 0.86 mm long, 0.15 mm wide, nonserrate except for very fine serrations on distal fifth, tapered rapidly subbasally to 0.12 mm wide, then parallel sided, extreme apex broad and bluntly rounded. Spermathecae not examined.

Distribution.—*Anastrepha anomoiae* is known from Panama and Colombia.

Comments.—The terminalia of the holotype were previously dissected and slide mounted. Abdominal segments 4–6 were damaged and mostly lost and the oviscape was broken, but the other parts of the terminalia are in good condition. The spermathecae are not on the slide and may have been lost or they may be inside the remainder of the abdomen.

Biology.—The host plants of this species are unknown.

Etymology.—The name of this species, a noun in apposition, is derived from the genus *Anomoia,* which it resembles in wing pattern.

Type data.—Holotype ♀ (USNM50456), COLOMBIA: Boyacá: Guaguaqui [probably Rio Guaguaqui, 5°46′N 74°29′W] [without date or collector]. Paratype ♂ (USNM50457), PANAMA: Coclé: El Valle [8°36′N 80°08′W], 829 m, 25 May 1983, blacklight, P.J. Spangler, R.A. Faitoute & W.E. Steiner.

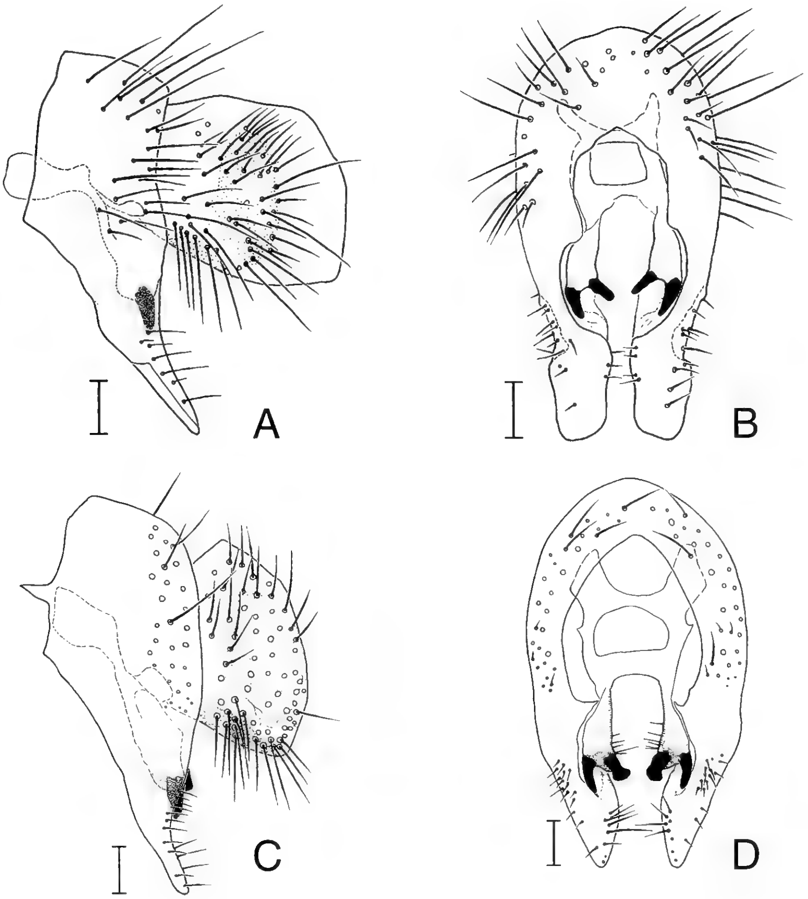

Fig. 6. Epandrium and surstyli, lateral and posterior views. A–B, *Anastrepha ornata* (USNM53042, ECUADOR: Ambato). C–D, *A. pulchra* (USNM52981, Panama: Arraijan).

Anastrepha bistrigata Bezzi
(Figs. 1A, 2D, 4E–F, 10E)

Anastrepha bistrigata Bezzi 1919a: 7 [description, host], 1919b: 372 [additional type data]; Lima 1934: 505 [taxomomy]; Stone 1942: 31 [revision]; Zucchi 1978: 35 [Brazil]; Korytkowski and Ojeda 1968: 52 [Peru; probably misidentification]; Foote 1967: 8 [in catalog]; Steyskal 1977: 5 [in key]; Morgante et al. 1980: 623 [isozymes]; Steck and Malavasi 1988: 1,004 [larva]; Steck et al. 1990: 343 [in larval key]; Solferini and Morgante 1987: 232, 1990: 201 [karyotype]; White and Elson-Harris 1992: 131 [taxonomy, pest status]; Matioli et al. 1992: 35 [isozymes]; Norrbom et al. 1999a: 77 [in catalog]; Malavasi and Zucchi 2000 [taxonomy, Brazil]; Norrbom, in press [host database].

Recognition.—*Anastrepha bistrigata* differs from all other species of *Anastrepha* except *A. striata* in having the dorsal posterior margin of the epandrium with a narrow, V-shaped, medial indentation, and by the following combination of characters: mesonotum with large, somewhat U-shaped, brown area, narrowed at transverse suture, but without other brown markings; mediotergite and subscutellum entirely brown or at least brown laterally; thoracic pleuron and abdomen without brown areas;

and scutum microtrichose, with broad nonmicrotrichose stripe on dorsocentral line, sometimes interrupted at transverse suture. These two species share additional characters, including: wing bands, particularly middle section of S-band, mostly orange brown; cell br with hyaline area posterior to pterostigma extending width of cell, reaching vein R_{4+5}; aculeus tip broad, at least 0.17 mm wide, and bluntly triangular; and lateral surstylus with rounded subapical lateral lobe. *Anastrepha bistrigata* differs from *A. striata* as indicated in the key and also in having a longer aculeus tip (0.35–0.40 vs. 0.24–0.31 mm) and a slightly shorter and stouter lateral surstylus that is slightly divergent distally from the opposite surstylus. The scutal microtrichia are less dense and not as white in appearance in oblique anterior view as in most *A. striata,* and the wing bands are usually slightly browner.

Description.—Largely orange with dark brown and yellow markings. Setae red-brown to dark brown. *Head:* Yellow except ocellar tubercle brown. Facial carina, in profile, concave. 3–5, usually 4, frontal setae; 2 orbital setae, posterior seta well developed. Ocellar seta weak and small or minute. Antenna extended 0.70–0.80 distance to lower facial margin. *Thorax* (Fig. 1A): Mostly orange with following areas yellow and often contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally at most half distance from level of acrostichal seta to that of dorsocentral seta; sublateral vitta extended from transverse suture almost to posterior margin, including intra-alar seta; scutellum except extreme base of disc (brown area well separated from basal seta); propleuron; dorsal margin of anepisternum; dorsal half of greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal pattern with following orange areas: broad area bordering medial vitta, large sublateral presutural area, broad area bordering mesal margin of sublateral vitta, and area lateral to sublateral vitta except extreme posterior margin. Dark brown, somewhat U-shaped mark narrowed, but not interrupted at transverse suture. Darker areas of pleuron orange. Subscutellum and mediotergite dark brown, narrowly orange medially. Mesonotum 2.91–3.52 mm long. Scutum microtrichose except for short medial presutural bare area extended no more than one third distance to transverse suture and broad stripe between medial and sublateral vittae, including dorsocentral seta, narrowed or narrowly interrupted at transverse suture; setulae mostly yellow medially, mostly pale to moderate brown on and lateral to nonmicrotrichose area. Katepisternal seta moderately developed, weaker but longer than postocellar seta, brown. *Wing* (Fig. 2D): Length 6.58–8.15 mm. Vein M strongly curved apically; section between BM-Cu and R-M 2.05–2.43 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.72–0.89 times as long as DM-Cu. Crossvein DM-Cu oblique, with anterior end more distal than posterior end. Pattern mosly pale to moderate brown or orange brown. C-band and S-band narrowly to broadly connected along vein R_{4+5}, but separated basally by hyaline area extending width of cell br and aligned with pterostigma, and covering basal fifth to third of cell dm and all of cell bm. C-band with cell bc and most of posterior half of cell c yellowish to subhyaline, and large yellow area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally to or almost to level of apex of vein R_1; anterior margin of band, including most of pterostigma, narrow distal margin, and base of cell br moderate brown. S-band largely yellow in cells dm and br, yellow area broadly extended to R-M and vein R_{4+5}; middle section of band anterior to vein R_{4+5} brown, usually with orange brown areas within it; distal section of band slender, at apex of vein R_{2+3} 0.36–0.44 times width of cell r_{2+3}; separated from

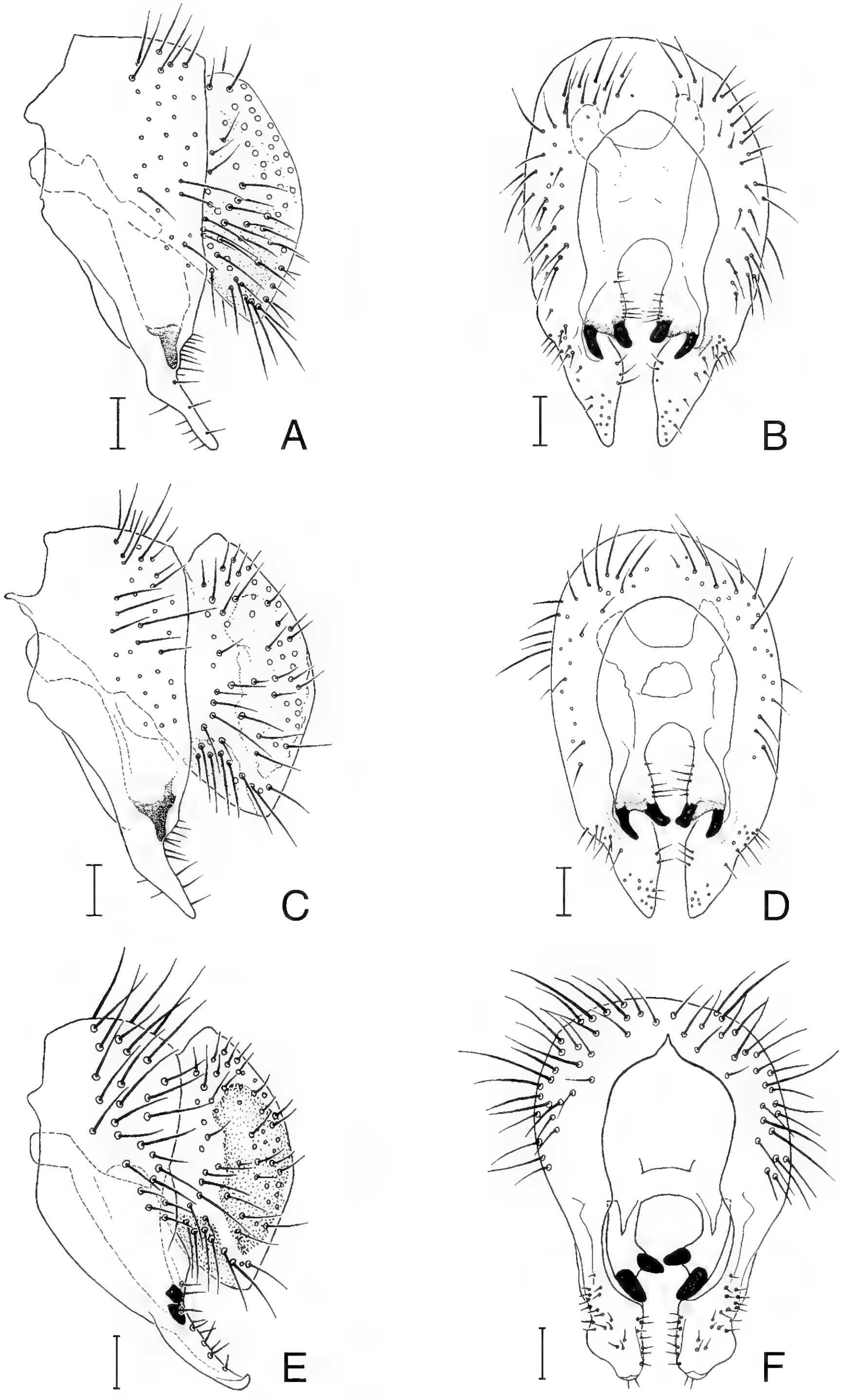

Fig. 7. Epandrium and surstyli, lateral and posterior views. A–D, *Anastrepha serpentina* (USNM53025, Brazil: Manaus, Boa Vista Rd.; and USNM53034, USA: Texas, McAllen). E–F, *A. striata* (USNM53079, Trinidad: Irois).

apex of vein M. Hyaline spot in cell r_1 nearly triangular, usually extended to vein R_{4+5}, sometimes interrupted in cell r_{2+3}; its apex aligned distinctly basal to R-M. V-band with distal arm present, complete or often partially or entirely weak or absent in cell r_{4+5}; proximal arm extended to vein R_{4+5}, sometimes faintly in anterior half of cell r_{4+5}, separated from S-band; extended basally along posterior wing margin almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen* (Fig. 1A): Mostly orange; posterior margins of tergites narrowly yellow, this area narrower laterally and also on successive tergites, nearly absent on tergite 5 and female tergite 6. *Male terminalia* (Figs. 4E–F): Dorsal posterior margin of epandrium with narrow, V-shaped, medial indentation. Lateral surstylus moderately long, slightly divergent from midline distally; basally with narrow, posteriorly projecting ridge bordering medial surstylus; in lateral view slightly posteriorly curved, extreme apex with small but strong posterior projection; in posterior view without strong basolateral lobe, main part somewhat triangular, with rounded subapical lateral lobe. Proctiger with lateral fold separating sclerotized areas. Phallus 4.45 mm long; 1.53 times as long as mesonotum. Glans 0.50 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 3.20–3.79 mm long, 0.97–1.09 times as long as mesonotum (Fig. 1A). Eversible membrane with 70–80 large, hook-like dorsobasal scales in triangular pattern. Aculeus 3.12–3.62 mm long; tip (Fig. 10E) 0.35–0.40 mm long, 0.18–0.20 mm wide, nonserrate, broadly triangular and blunt apically. Spermathecae ovoid to pear-shaped.

Distribution.—This species is known only from southern Brazil (Goiás, Rio de Janeiro, Minas Gerais, São Paulo, Santa Catarina) (Lima 1934, Zucchi 1978, Malavasi and Zucchi 2000). Korytkowski and Ojeda (1968) reported *A. bistrigata* from Peru based on a single male, but their illustrations of the mesonotum (Fig. 18) and terminalia of this specimen suggest that it was misidentified.

Biology.—The reported native host plants include three species of *Psidium* (Myrtaceae): *P. australe* Cambess., *P. guajava* L., and *P. guineense* Sw. (= *P. araca* Raddi), and one species of Sapotaceae, *Pouteria gardneriana* (A. DC.) Radlk. (Malavasi and Zucchi 2000; see Norrbom, in press, for full list of records). The record of *Mangifera indica* L. (Anacardiaceae) (Korytkowski and Ojeda 1968) is doubtful, but it is not a native host if it is in fact attacked by *A. bistrigata.*

Comments.—Selivon and Morgante (1997) discussed the mating behavior of *A. bistrigata* and its reproductive isolation from *A. striata.*

Type data.—Lectotype [here designated to fix and stabilize the current concept of the name] ♀ (MCSNM), with the following handwritten labels: [red ink on white label] "58."; "S. Paolo Barbiellini"; and "Lectotype ♀ Anastrepha bistrigata Bezzi by Norrbom 2001." Bezzi (1919a, b) stated that he described this species from 1 ♂ and 2 ♀ syntypes from Brazil: São Paulo: Baurú, reared ex. fruit of "araxà" [*Psidium guineense* Sw.], A. A. Barbiellini. The paralectotypes are labeled similar to the lectotype, except that the male has the number "59" and the female "57," and the latter also has "Brasile" on its second label. There is also a damaged male of another *Anastrepha* species, possibly *A. fraterculus,* on the pin of the female.

Other specimen data.—BRAZIL: Goiás: Veadeiros, 30 Apr 1956, F. S. Truxal, 1 ♀ (LACM USNM53051). Minas Gerais: Belo Horizonte, reared from goiabas [*Psidium guajava* L.], 3 Sep 1934, O. Monte, 1 ♀ (USNM53050). São Paulo: São Paulo, on guava, 11 Dec 1931, M. Kisliuk & C.E. Cooley, 1 ♀ (USNM53049); Univ. of São Paulo (Malavasi/Morgante) culture initiated from larvae reared from guava from Campinas, Nov 1986, G.J. Steck, 1 ♂, 1 ♀ (USNM53047–8); same, 5 Jun 1991, 1 ♀ (USNM53046).

Anastrepha normalis Norrbom, new species

(Figs. 1B, 2F–G, 5A–B, 8C, 9C, 10F)

Anastrepha anomala: Stone 1942: 29 [in part]; Caraballo 1981: 60 [Venezuelan specimens, host].

Anastrepha sp.: Boscán et al. 1980: 61 [host].

Anastrepha n. sp. nr. *anomala:* McPheron et al. 1999: 346.

Recognition.—*Anastrepha normalis* is one of the species of the *serpentina* group with a hyaline area in cell br posterior to the pterostigma that is not extended to vein R_{4+5}. It differs from the other species with this character in having a paler wing pattern. In particular, the middle section of the S-band anterior and distal to crossvein R-M is orange brown with only narrow dark brown margins. *A. normalis* further differs from all of these species, except *A. ornata* and one female of *A. anomala* (Maranhão, Brazil) in lacking fine serrations on the aculeus tip (Fig. 10F). It is most likely to be confused with *A. anomala* or *A. pseudanomala,* from which it further differs in having the aculeus tip less than twice as long as wide. It differs further from *A. anomala* in lacking the basolateral lobe on the lateral surstylus and from *A. pseudanomala* in having the distal section of the S-band slightly broader and sometimes touching the apex of vein M.

Description.—Largely dark orange to dark red brown with yellow markings. Setae dark brown. *Head:* Yellow except ocellar tubercle brown. Facial carina, in profile, concave. 3–5, usually 4, frontal setae; usually 2 orbital setae, posterior seta absent on one side in 4 and on both sides in 3 of 29 specimens examined. Ocellar seta weak and small or minute. Antenna extended 0.70–0.85 distance to lower facial margin. *Thorax* (Fig. 1B): Mostly dark orange to dark red brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally only slightly beyond level of acrostichal seta (at most half distance to level of dorsocentral seta); sublateral vitta extended from transverse suture to or almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area well separated from basal seta); propleuron; dorsal margin and anteroventral corner of anepisternum; greater ampulla and often bordering area of anepimeron; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal pattern with broad orange area bordering medial vitta, large orange sublateral presutural area, usually with narrow orange area of varying length bordering mesal margin of sublateral vitta. Darker areas of anepisternum and anepimeron mostly dark brown. Those of meron and katatergite dark orange or dark brown. Darker area of katepisternum orange. Subscutellum and mediotergite dark brown, narrowly orange medially. Mesonotum 3.41–3.74 mm long. Scutum microtrichose except for broad presutural bare area extended about midway to transverse suture; setulae mostly yellow. Katepisternal seta weak, shorter than postocellar seta, yellowish. *Wing* (Figs. 2F–G): Length 7.24–8.15 mm. Vein M strongly curved apically; section between BM-Cu and R-M 2.51–2.75 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.69–0.76 times as long as DM-Cu. Crossvein DM-Cu oblique, with anterior end more distal than posterior end. Pattern mostly brown and pale to dark orange brown. C-band and S-band broadly connected in cell br and often in r_{2+3}, but separated basally by hyaline area in posterior ⅔ of br aligned with pterostigma, usually a small basal hyaline area in cell dm, and hyaline to yellowish area covering all of cell bm. C-band with cell bc and posterior half to ⅔ of cell c yellowish to subhyaline, and large yellow area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, gradually merging with orange brown distal part

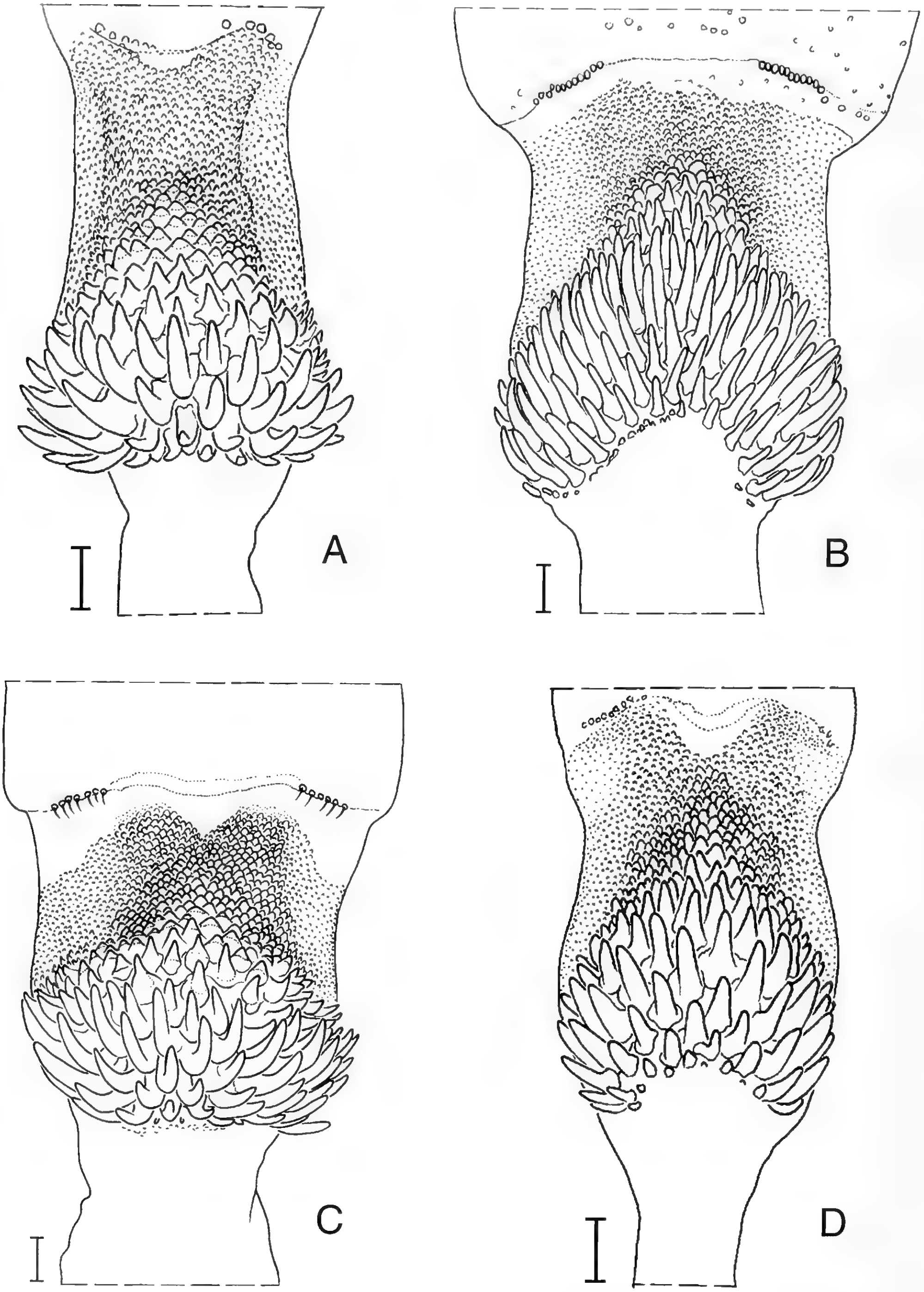

Fig. 8. Eversible membrane, dorsobasal scales. A, *Anastrepha anomala* (USNM52951, Panama: Arraijan). B, *A. anomoiae* (holotype). C, *A. normalis* (USNM52939, Venezuela: Marcillal de la Costa). D, *A. pseudanomala* (USNM50455, Costa Rica: 20 km. S Upala).

of band; margins of band, including most of pterostigma moderate brown. S-band largely yellow to orange in cell dm, darkening to orange brown anteriorly but middle section of band brown only narrowly on margins; distal section of band moderately broad, at apex of vein R_{2+3} 0.51–0.64 times width of cell r_{2+3}; separated from or extended to apex of vein M. Hyaline spot in cell r_1 nearly triangular, extended well into cell r_{2+3}, sometimes reaching vein R_{4+5}; its apex aligned slightly basal to R-M. V-band with distal arm usually absent, rarely represented by faint spot in cell M (1 ♂, 1 ♀ from Venezuela); proximal arm extended to vein R_{4+5}, usually separated from S-band but occasionally narrowly connected along R_{4+5}; extended basally along posterior wing margin often almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen* (Fig. 1B): Orange with yellow and brown markings. Syntergite 1+2 and tergite 3 each with brown band. Tergites 4–6 mostly orange. Posterior margin of tergites yellow, this area narrower laterally and also narrower on successive tergites, nearly absent on male tergite 5 and female tergite 6. *Male terminalia* (Figs. 5A–B): Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view very slightly curved; in posterior view without strong basolateral lobe, main part narrowly triangular, acute apically. Proctiger with lateral fold separating sclerotized areas. Phallus 5.11–5.42 mm long; 1.50–1.53 times as long as mesonotum. Glans 0.40 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 3.79–4.41 mm long, 1.07–1.21 times as long as mesonotum. Eversible membrane (Fig. 8C) with 40–50 large, hook-like dorsobasal scales in triangular pattern. Aculeus 3.62–4.14 mm long; tip (Figs. 9C, 10F) 0.23–0.28 mm long, 0.13–0.15 mm wide, gradually tapered and nonserrate. Spermathecae ovoid or teardrop shaped.

Distribution.—*Anastrepha normalis* is known from Panama and Venezuela.

Etymology.—The name of this species is an adjective referring to the more normal color of the wing pattern (i.e., more common in *Anastrepha* in general) compared to that of the closely related *A. anomala.*

Biology.—*Lacmellea panamensis* (Woodson) Markgr. (Apocynaceae) is probably the only known host. Boscán et al. (1980) reared an *Anastrepha* sp. from "chirica," which they reported as *Jaquinia revoluta* Jacq. (= *J. armillaris* Jacq.) (Theophrastaceae) and Caraballo (1981) identified these fly specimens as *A. anomala* without giving a scientific name for "chirica." I reexamined several specimens of this series and found them to be *A. normalis.* Because chirica is a common name for *L. panamensis* (see Type data), and the related species *A. anomala* is also known from this host, it seems likely that all of the Venezuelan records pertain to this plant.

Type data.—Holotype ♀ (IZAM, USNM52943), VENEZUELA: Falcón: Marcillal [11°12′N 68°50′W], 125 m, 7 May 1993, K.P. Katiyar, reared ex. fruit *Zschokkea panamensis* [= *Lacmellea panamensis*] ("chirica"), MFAPK-00345. Paratypes: PANAMA: Panamá: El Cermeño [8°44′N 79°51′W], 20 Jun 1939, J. Zetek 4465, 1 ♀ paratype *A. anomala* (USNM52949); same, J. Zetek 4467, 1 ♀ paratype *A. anomala* (IOC USNM53106); same, J. Zetek 4475, 1 ♀ paratype *A. anomala* (BMNH USNM53114); El Cermeño, 27 Jun 1939, J. Zetek 4489, 1 ♂ paratype *A. anomala* (USNM52960); El Cermeño, 2 Apr 1940, J. Zetek 4643, 1 ♀ (USNM52948). VENEZUELA: Falcón: Marcillal [11°12′N 68°50′W], 125 m, 7 May 1993, K.P. Katiyar, reared ex. fruit *Zschokkea panamensis* ("chirica"), MFAPK-00345, 1 ♂ (IZAM, USNM52944), 5 ♂, 8 ♀ (USNM47439–43, 47447–54), 1 ♂, 1 ♀ (BMNH, USNM52946–47), 1 ♂, 1 ♀ (MEUP, USNM47445–6), 1 ♂, 1 ♀ (ESALQ, USNM47444, 52945); Maicillal [sic] de la Costa, 200–550 m, ex. larva en frutos de chirica, 29 May 1967, R. Mendez & R. Bandres, 2 ♂, 2 ♀ (USNM52938–41), 42 ♂, 53 ♀ (IZAM).

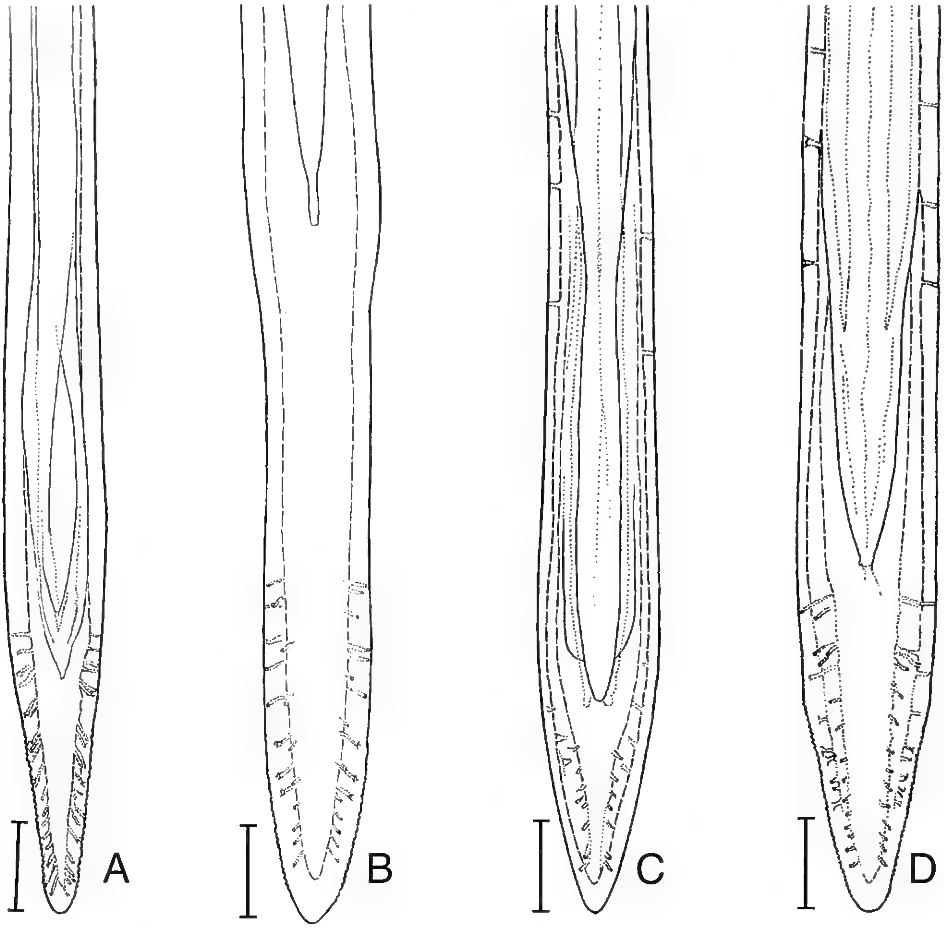

Fig. 9. Aculeus, apical part, ventral view. A, *Anastrepha anomala* (USNM52951, Panama: Arraijan). B, *A. anomoiae* (holotype). C, *A. normalis* (USNM52939, Venezuela: Marcillal de la Costa). D, *A. pseudanomala* (USNM50455, Costa Rica: 20 km. S Upala).

Anastrepha ocresia (Walker)
(Figs. 1C, 2H, 5C–D, 10G)

Trypeta ocresia Walker 1849: 1016 [description]; Loew 1873: 231 [taxonomy].

Trypeta (*Acrotoxa*) *ocresia:* Loew 1873: 337 [taxonomy]; Osten Sacken 1878: 189, 195 [in catalog].

Acrotoxa ocresia: Loew 1873: 231 [taxonomy].

Anastrepha ocresia: Aldrich 1905: 602 [in catalog]; Bezzi 1909: 283 [in catalog and key]; Hendel 1914: 14 [in key]; Greene 1934: 158 [review]; Stone 1942: 24 [revision]; Aczél 1950: 221 [in catalog]; Foote 1964: 322 [type data], 1965: 673 [in catalog]; Weems 1968: 1 [review, habitus illustration, hosts]; Wasbauer 1972: 107 [host list]; Steyskal 1977: 8 [in key]; Norrbom and Kim 1988: 51 [host list]; White and Elson-Harris 1992: 148 [taxonomy, pest status]; Foote et al. 1993: 103 [taxonomy]; Fernández et al. 1998: 34 [Cuba, host]; Norrbom et al. 1999a: 81 [in catalog]; Norrbom, in press [host database].

Anastrepha ochresia: Foote 1967: 14 [in catalog; misspelling].

Trypeta tricincta Loew 1873: 225 [description]; Stone 1942: 24 [synonymy].

Trypeta (*Acrotoxa*) *tricincta:* Loew 1873:

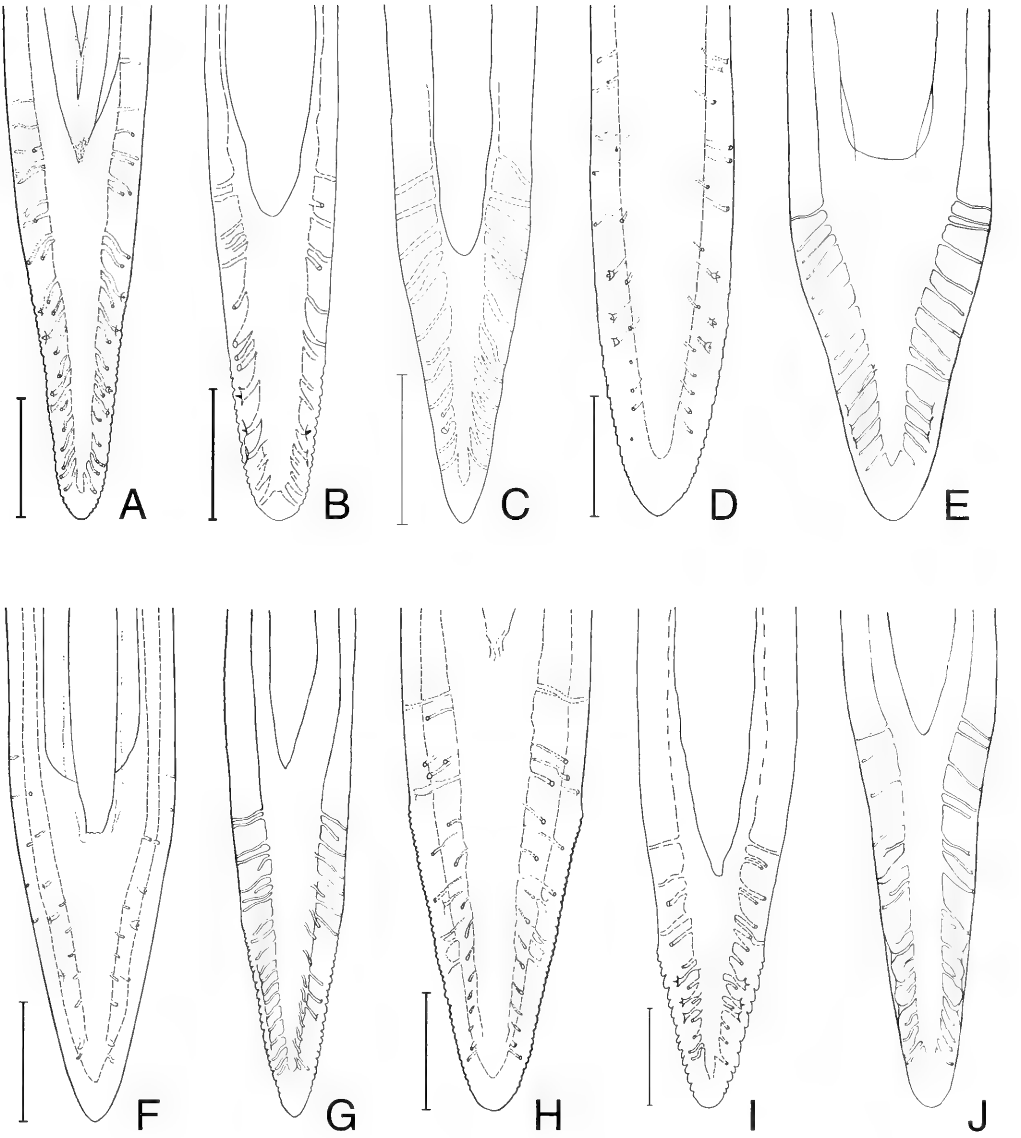

Fig. 10. Aculeus tip, ventral view. A–C, *Anastrepha anomala* (USNM52951, Panama: Arraijan; USNM53107, Brazil: Cruz das Almas; Brazil: Itapecuru-Mirim, USNM31431). D, *A. anomoiae* (holotype). E, *A. bistrigata* (copied from Stone 1942, fig. 3B). F, *A. normalis* (USNM52939, Venezuela: Marcillal de la Costa). G, *A. ocresia* (copied from Stone 1942, fig. 1E). H, *A. pseudanomala* (USNM50455, Costa Rica: 20 km. S Upala). I, *A. pulchella* (USNM51717, Panama: El Cermeño). J, *A. pulchra* (copied from Stone 1942, fig. 2B).

329 [classification]; Osten Sacken 1878: 189 [in catalog].

Acrotoxa tricincta: Loew 1873: 227 [classification].

Anastrepha tricincta: Aldrich 1905: 602 [in catalog]; Bezzi 1909: 284 [in catalog and key]; Hendel 1914: 14 [in key].

Recognition.—*Anastrepha ocresia* is one of the species of the *serpentina* group with a hyaline area in cell br posterior to the pterostigma that is not extended to vein R_{4+5}. It differs from all other species of the *serpentina* group in having the brown markings of the mesonotum restricted to the areas near the scuto-scutellar suture, and the scutum without microtrichia except on extreme lateral margin. The broad distal section of the S-band (at apex of vein R_{2+3} greater than 0.70 times width of cell r_{2+3}) differentiates it from all other species except *A. ornata.* The distal arm of the V-band is always partially present, at least from vein M to posterior wing margin. *A. ocresia* is the only species of the *serpentina* group known from the Greater Antilles and Florida.

Description.—Largely orange to red brown with yellow and dark brown markings. Setae dark brown. *Head:* Yellow except ocellar tubercle brown. Facial carina, in profile, concave. 3–5, usually 4, frontal setae; 1–2 orbital setae, posterior seta absent on at least one side in 9 of 25 specimens, but well developed if present. Ocellar seta weak, short to minute. Antenna extended 0.70–0.85 distance to lower facial margin. *Thorax* (Fig. 1C): Mostly orange with following areas yellow and usually distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the medial vitta extended nearly full length of scutum, anterior ¾ very slender, broadened posteriorly, but extended laterally only to or slightly beyond level of acrostichal seta; sublateral vitta extended from transverse suture to posterior margin, including intra-alar seta; scutellum except base (brown area well separated from basal seta or sometimes diffusely extended to it or slightly beyond); dorsal margin and anteroventral corner of anepisternum; dorsal half to ⅔ of greater ampulla; katepimeron; and most of anatergite and katatergite. Mesonotum mostly to entirely orange, usually with dark brown spot or band bordering scuto-scutellar suture, sometimes shaped like shallow U, the arms extended anteriorly no more than to level of intra-alar seta. Darker areas of anepisternum, katepisternum, and anepimeron orange; those of meron and katatergite sometimes dark brown. Subscutellum and mediotergite usually dark brown, narrowly orange medially, but occasionally mostly orange with dark brown lateral margins. Mesonotum 2.50–3.45 mm long. Scutum without microtrichia except postsutural lateral margin (lateral to supra-alar seta); presutural setulae mostly yellow, brown on narrow area along dorsocentral line, postsutural setulae yellow medially, mostly brown lateral to level of acrostichal seta. Katepisternal seta usually slightly longer than postocellar seta, usually moderately developed but occasionally weak, red brown or occasionally yellowish. *Wing* (Fig. 2H): Length 5.27–7.49 mm. Vein M strongly curved apically; section between BM-Cu and R-M 1.85–2.33 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.80–0.96 times as long as DM-Cu. Crossvein DM-Cu oblique, with anterior end more distal than posterior end. Pattern mostly moderate to dark brown. C-band and S-band narrowly to broadly connected in cell br and sometimes r_{2+3}, separated basally by hyaline area in cell br aligned with pterostigma, hyaline basal ¼–⅓ of cell dm, and hyaline to yellowish area covering all of cell bm. C-band yellowish or subhyaline in cells bc and cell c, except anterior margin; with large yellowish area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally at least to apical ⅔ of pterostigma, sometimes reaching level of apex of vein R_1. S-band with narrow yellow area in cell dm; most of cell bcu yellowish to subhyaline; rest of band brown, including areas distal to and anterior to R-M; distal section broad, at apex of vein R_{2+3} 0.73–1.00 times width of cell r_{2+3}; extended to or occasionally almost to apex of vein M. Hyaline spot in cell r_1 usually nearly triangular, sometimes rounded, usually extended into cell r_{2+3} and often to vein R_{4+5}; its apex aligned slightly to distinctly basal to R-M. V-band with distal arm usually reduced, extended anteriorly beyond vein M, but only rarely reaching vein R_{4+5} (one female from Dominican Republic); separated from proximal arm or sometimes connected along vein M (if connected, never with hyaline space between band and vein M); proximal arm usually extended to vein R_{4+5}, occasionally connected to S-band along vein R_{4+5}; extended basally along posterior wing margin often almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen* (Fig. 1C): Orange with yellow and brown markings. Syntergite 1+2 and tergites 3–4 with narrow brown bands, narrowly medially interrupted occasionally on tergite 3, often on tergite 4; posterior margin yellow. Tergite 5 and female tergite 6 orange. *Male terminalia* (Figs. 5C–D): Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view slightly curved; in posterior view with strong basolateral lobe, main part narrowly triangular, acute apically. Proctiger with lateral fold separating sclerotized areas. Phallus 3.54–4.51 mm long; 1.27–1.60 times as long as mesonotum. Glans 0.50 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 2.95–4.00 mm long, 0.95–1.32 times as long as mesonotum. Eversible membrane with 25–40 large, hook-like dorsobasal scales in triangular pattern. Aculeus 2.83–4.08 mm long; tip (Fig. 10G) 0.30–0.36 mm long, 0.11–0.13 mm wide, very gradually tapered basally, apical 0.53–0.67 finely serrate, triangular. Spermathecae ovoid.

Distribution.—*Anastrepha ocresia* is known from the USA (Florida Keys), Cuba, Hispaniola, Puerto Rico, and Jamaica. The only records from the Florida Keys are from 1936, and *A. ocresia* may not be currently established there.

Biology.—The native host plants of *A. ocresia* are uncertain. It has been reared several times from *Manilkara zapota* (L.) P. Royen (Sapotaceae) (Foote 1964, as *Achras zapota*; Fernández et al. 1998), but this plant is not native to the Greater Antilles. Weems (1968) listed *Psidium guajava* L. (Myrtaceae) as a host, but did not indicate the basis for this record, and the status of this plant as a host needs confirmation. *Citrus × paradisi* Macfad. (Rutaceae) was erroneously listed as a host plant by White and Elson-Harris (1992), citing Weems (1968), but the latter reported only an adult foliage record.

Type data.—*Trypeta ocresia:* Lectotype ♀ (BMNH), Jamaica, Mr. Gosse; designated by inference of holotype by Greene (1934: 158) [examined; with following labels: [square, handwritten] "Jam. [another word, possibly "Gosse"]"; [long, handwritten] "Ocresia 1016"; [handwritten, square] "Anastrepha ocresia Walk. Type"; [circular, green-bordered] "Type"; [red bordered] "LECTOTYPE Trypeta ocresia Walker by Greene 1934: 158, by inference of holotype"]. A female of *Anastrepha suspensa* (Loew) was in the BMNH collection with the lectotype, but is doubtfully a syntype because Walker mentioned the incomplete V-band in the original description ("a forked stripe, which is imperfect, nearly half of the tip fork being wanting") and it is complete in this specimen. However, because Walker described *T. ocresia* from an unstated number of female specimens it is best to regard Greene's (1934) discussion of "the type female" as a lectotype designation. According to Papavero (1973: 247) P. H. Gosse collected in Jamaica between 6 December 1844 and 11 July 1846.

Trypeta tricincta: Lectotype ♂ (MCZ), on shipboard, 60 mi. NW of St. Nicholas [probably Môle St.-Nicolas], Haiti, P. R. Uhler; designated by inference of holotype by Greene (1934: 146) [examined; with following labels: "60 miles N. W. of St. Nicolas, Hayti, P. R. Uhler, on shipboard"; "tricincta Lw."; [red] "Type 13282"; [red bordered] "LECTOTYPE Trypeta tricincta Loew by Greene 1934: 146, by inference of holotype"].

Other specimen data.—CUBA: Baracoa de Banta, on mango, 19 Jun 1930, E. Kostal, 1 ♀ (MCZ USNM50477). Guantánamo: Guantánamo Bay Naval Base, McPhail Trap, 11 Dec 1975, 1 ♂ (USNM52992). Isla de la Juventud [unspecified locality], Jun 1924, Moznette, 1 ♀ (TAMU USNM52963). Matanzas: Central Conchita [= Puerto Rico Libre, 22°44′N 81°32′W], reared from *A. sapota* [= *Manilkara zapota*], 25 Jun 1946, L.C. Scaramuzza, 2 ♀ (USNM50474–5); same, reared 2–7 Jul 1946, from larvae collected 25 Jun 1946, 3 ♂, 6 ♀ (USNM52994–53002). Pinar del Río: Péninsula de Guanahacabibes, Bolondron [21°52′28N 84°49′51W], 11 Apr 1924, S.C. Bruner no. 9041, 1 ♂ (MCZ USNM50476); same, 11 Mar 1924, 1 ♀ (USNM51712). DOMINICAN REPUBLIC: [unspecified locality], reared ex. *Achras sapota* [= *Manilkara zapota*], Aug 1962, 2 ♂, 7 ♀ (USNM50464–72), 1 ♀ (MCZ USNM50463). Barahona: near Filipinas Larimar Mine, near La Travesia [18°07′N 71°07′W], at light, 20–26 Jun 1992, R. E. Woodruff & P. E. Skelly, 1? (FSCA USNM51780). Distrito Nacional: Santo Domingo, 22 Jul 1919, H. Morrison, 1 ♀ (USNM50473). La Altagracia: Bayahibe, 2 km N of, 18°23′N 68°51′W, 10 m., 3 Jul 1992, C. Young, R. Davidson, S. Thompson, J. Rawlins, 1 ♀ (USNM51938); Higuey, La Gima Colon [possibly La Jina (18°42′N 68°37′W)], 730 m., McPhail trap in *Citrus sinensis,* 24 July 1990, C.W. Forster, 2 ♂, 3 ♀ (USNM50458–62). Pedernales: Cabo Rojo, 26 km N of, 18°6′N 71°38′W, 730 m., wet deciduous forest, sweep sample, 13–25 Jul 1990, L. Masner, J. Rawlins, C. Young, 1 ♂ (CMP USNM51939); Cabo Rojo, Alcoa plant, 100 ft., blacklight trap, 3 Jul 1998, R. E. Woodruff & R. M. Baranowski, 1 ♀ (USNM51771). JAMAICA: [unspecified locality], 9 Jul, Avinoff & Schoumatoff, 1 ♀ (CMP USNM52993); Manchester: [unspecified locality], 25 Feb 1986, D. Enkerlin, 1 ♀ (USNM52990). Saint Thomas: [unspecified locality], 14–21 Feb 1986, R.C. Murray, 1 ♀ (USNM52991). USA: Florida: Monroe Co., Key Largo, Rock Harbor, trap in sapodilla tree, 3 Jul 1936, Barcus & Stirling, 1 ♀ (USNM53003); Key West, 28 Mar 1936, (FSCA) [Stone 1942: 25, Weems 1968: 1; specimens not examined].

Anastrepha ornata Aldrich
(Figs. 1D, 2I, 6A–B, 11A)

Anastrepha ornata Aldrich 1925: 6 [description, Ecuador]; Lima 1934: 495, 556 [in key]; Stone 1942: 25 [revision, hosts]; Aczél 1950: 222 [in catalog]; Oakley 1950: 178 [host list]; Campos 1960: 51 [hosts]; Foote 1967: 14 [in catalog]; Steyskal 1977: 8 [in key]; Norrbom and Kim 1988: 51 [host list]; Yepes and Vélez 1989: 82 [Colombia, host]; Molineros et al. 1992: 34, 36 [Ecuador, host]; White and Elson-Harris 1992: 148 [taxonomy, pest status]; Tigrero 1998: 24 [Ecuador, hosts]; Norrbom et al. 1999a: 81 [in catalog]; Norrbom, in press [host database].

Anastrepha odonata: Hedström 1987: 373 [Ecuador, host; misspelling].

Recognition.—*Anastrepha ornata* differs from all other species of *Anastrepha* in having the middle section of the S-band very slender, but the distal section broad. It is unusual in having the proximal arm of the V-band connected along the posterior wing margin to a basal extension of the S-band along vein A_1+Cu_2; within the *serpentina* group this occurs only in some *A. pulchella. A. ornata* further differs from the other species of the *serpentina* group in having the C-band and S-band well separated. It is one of the species with the thoracic pleuron largely brown and with the abdomen partially brown. It differs from the other predominantly brown species in having broad dorsocentral nonmicrotrichose areas on the scutum and the aculeus tip broadly triangular.

Description.—Largely dark orange to dark brown with yellow markings. Setae dark brown. *Head:* Mostly yellow. Ocellar tubercle brown. Frons often with small brown marks bordering orbital plate laterally and mesally, rarely with orbital plate also brown; occasionally orange to red-brown medially or anteromedially. Occiput with paired, triangular or rounded, brown mark dorsally. Facial carina, in profile, concave. 3–4 frontal setae; 2 orbital setae, posterior seta well developed. Ocellar seta weak, small to minute. Antenna extended 0.70–0.85 distance to lower facial margin. *Thorax* (Fig. 1D): Mostly orange brown to

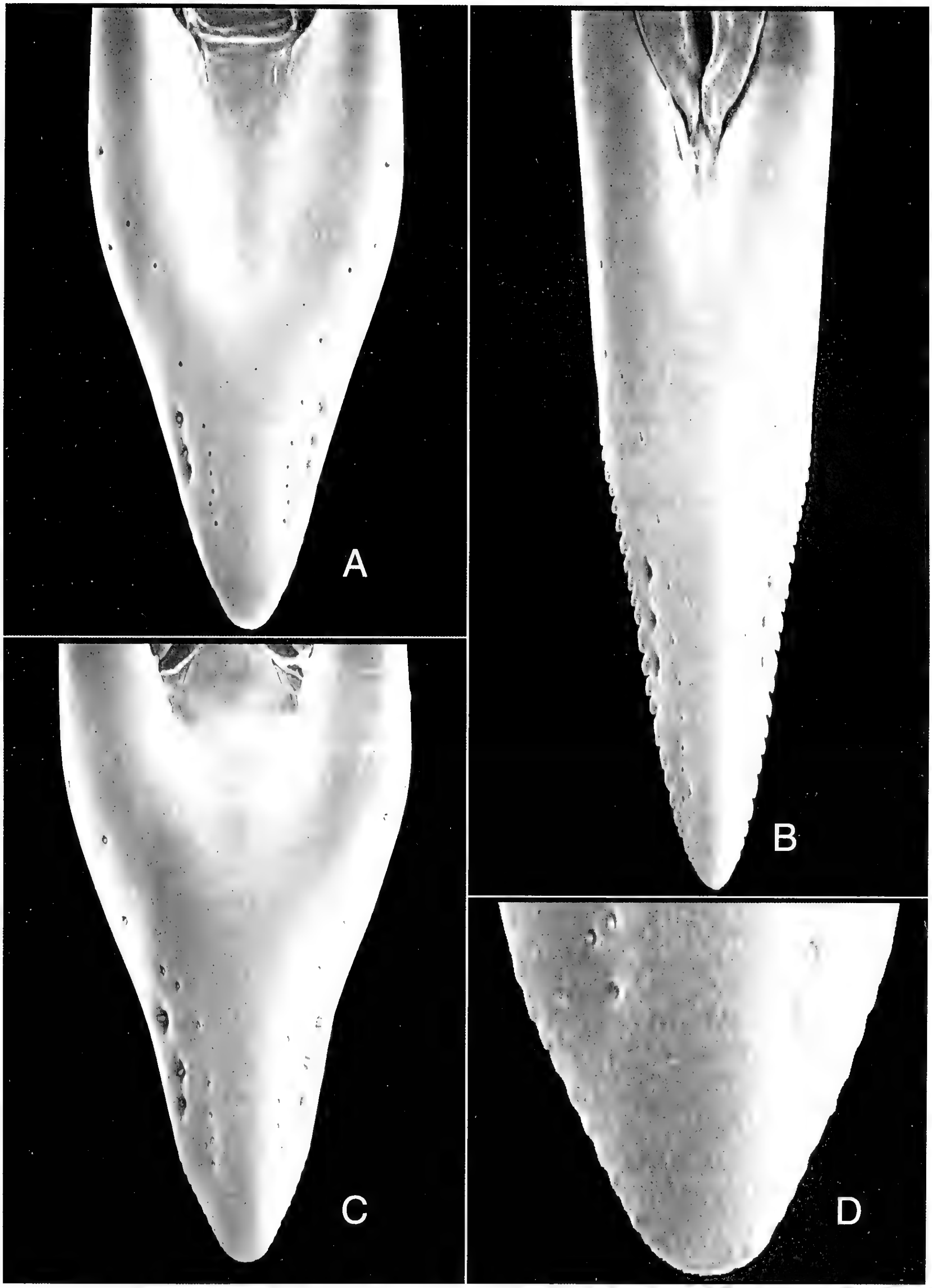

Fig. 11. Aculeus tip, ventral view, scanning electron micrograph. A, *Anastrepha ornata* (USNM53043, Ecuador: Ambato). B, *A. serpentina* (USNM53099, Panama: Balboa). C, *A. striata* (USNM53103, Colombia: Aljibes). D, *A. striata*, apex enlarged.

brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, extended laterally about half distance from acrostichal seta to dorsocentral seta; sublateral vitta extended from transverse suture to or almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area usually well separated from basal seta, but sometimes narrowly separated); dorsal margin and anteroventral corner of anepisternum; dorsal half of greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal darker areas mostly red brown to dark brown, with short to moderately long, moderately broad, usually truncate, orange submedial area bordering or partially touching medial vitta and crossing transverse suture. Darker areas of anepisternum, anepimeron, meron, and katatergite dark brown. Katepisternum usually orange on anteroventral margin, brown posteriorly. Subscutellum and mediotergite red brown to dark brown, sometimes narrowly orange medially. Mesonotum 2.75–3.45 mm long. Scutum without microtrichia anterior to transverse suture except on and between orange submedial areas and narrowly along suture and lateral margin, microtrichose posterior to transverse suture except for broad sublateral stripe between dorsocentral and intra-alar lines; setulae brown anteriorly and laterally, yellow on and between submedial orange areas and to varying degrees posterior to them. Katepisternal seta moderately developed, weaker than but usually longer than postocellar seta, brown. *Wing* (Fig. 2I): Length 6.91–8.23 mm. Vein M strongly curved apically; section between BM-Cu and R-M 1.81–2.51 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.76–0.91 times as long as DM-Cu. Crossvein DM-Cu distinctly oblique, with anterior end more distal than posterior end. Pattern mostly dark brown. C-band and S-band completely separated except sometimes for pale yellow area of S-band in cell dm narrowly bordering brown posterior part of C-band. C-band yellowish to subhyaline in cell bc and posterior half of cell c; with large yellowish area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally to end of band almost at level of apex of vein R_1. S-band with large, sometimes faint, yellow area covering most of basal half of cell dm; rest of band dark brown, including areas distal to and anterior to R-M; brown part of middle section of band narrow; distal section broad, at apex of vein R_{2+3} 0.53–1.00 times width of cell r_{2+3}, if relatively narrow at that point usually broader more distally; extended to or less commonly almost to apex of vein M. Cell bm hyaline. Cell br with large hyaline area posterior to pterostigma broadly connected to marginal hyaline area in cell r_1. V-band with distal arm absent; proximal arm slender, extended anteriorly to vein M, but at most to middle of cell r_{4+5} and usually fainter in the latter cell; separated from S-band anteriorly, but extended basally along posterior wing margin to vein A_1+Cu_2 and connected to extension from base of S-band. *Abdomen* (Fig. 1D): Orange with yellow and brown markings. Syntergite 1+2 mostly brown, with narrow medial yellow band and posterior margin broadly yellow, narrowing laterally. Tergites 3–4 with brown bands, occasionally narrowly medially interrupted on tergite 4; posterior margin yellow, narrowing laterally. Tergite 5 and female tergite 6 orange. *Male terminalia* (Figs. 6A–B): Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view slightly curved; in posterior view, without strong basolateral lobe, main part paddle-shaped, broad and truncate apically. Proctiger with lateral fold separating sclerotized areas. Phallus 3.75–4.37 mm long; 1.29–1.40 times as long as mesonotum. Glans 0.55 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 3.00–3.95 mm long, 1.03–1.19 times as long as mesonotum. Eversible membrane with 55–65 large, hook-like dorsobasal scales in triangular pattern. Aculeus 3.10–3.74 mm long; tip (Fig. 11A) 0.31–0.36 mm long, 0.16–0.18 mm wide, nonserrate, broadly triangular and blunt apically. Spermathecae globose to elongate ovoid.

Distribution.—*Anastrepha ornata* is known from Colombia and Ecuador. There is only a single previous record from Colombia (Yepes and Vélez 1989). In Ecuador, *A. ornata* has been reported from the provinces of Azuay, Chimborazo, Morona-Santiago, Napo, Pastaza, Pichincha, and Tungurahua (Stone 1942, Hedström 1987, Molineros et al. 1992, Tigrero 1998) and also occurs in Cotopaxi.

Biology.—The following plants have been reported as hosts of *A. ornata*: Myrtaceae—*Acca sellowiana* (O. Berg) Burret (Yepes and Vélez 1989, as *Feijoa sellowiana*); *Psidium guajava* L. (Campos 1960, Hedström 1987, Molineros et al. 1992, Tigrero 1998); *Syzygium jambos* (L.) Alston (Tigrero 1998, as *Eugenia jambos*); Rosaceae—*Prunus persica* (L.) Batsch (Campos 1960, as *Persica vulgaris*); and *Pyrus communis* L. (Stone 1942, Campos 1960). Of these, only *P. guajava* is a native host. *Pouteria lucuma* (Ruiz and Pav.) Kuntze (Sapotaceae) was reported as a host by Tigrero (1998), but the record he cited from Aldrich (1925) was clearly based on a specimen that was collected on the plant and not reared.

Type data.—Holotype ♀ (USNM52985), Ecuador: Oriente, Baños [probably Tungurahua: Baños (1°24′S 78°25′W)], 6,000 ft., 30 Oct 1922, F. X. Williams [examined].

Other specimen data.—COLOMBIA: Antioquia: Sonsón, La Ceja, in feijoa [reared ex. *Acca sellowiana*], Jul 1988, F. C. Yepes, 1 ♂ (USNM53036); La Ceja, 2,300 m, Jul 1997, E. Arevalo, EA48, 2 ♂, 2 ♀ (USNM5869–71, USNM51916); El Retiro, 2,200 m, Mar 1997, E. Arevalo, 10 ♂, 10 ♀ (USNM, BMNH, ESALQ, MEUP, USNM51850–69). ECUADOR: Cotopaxi: Las Pampas, 1,800 m, 16 Jul 1998, I. Tapia, 1 ♀ (USNM52513). Napo: Santa Rosa de Quíjos [0°18′S 77°46′W], 13 Nov 1986, I. Hedström, 1 ♀ (USNM52347). Tungurahua: Ambato [1°15′S 78°37′W], guayaba [*Psidium guajava*], 1 ♂, 3 ♀ (USNM53041–4); same, *Psidium* sp., F. Campos R., 1 ♂, 1? (USNM53037–8); same, in fruit *Pyrus communis,* F. Campos R., 1 ♂, 1 ♀ (USNM53039–40); Baños, Apr 1930, R. Benoist, 1 ♂ (MNHNP USNM52987); Baños, on Luma tree, 19 Jan 1923, F. X. Williams, 1 ♂ paratype (USNM53045); Baños, 20 km. W, 1,400 m, 15 Jul 1989, L. Stange & R. Miller, 1 ♀ (FSCA USNM52986); Puñapi [1°22′S 78°28′W], 2050 m, on *Psidium guajava* & *Prunus persica,* 12 Jan 1998, M. Lascano, 1 ♂ (USNM52512).

***Anastrepha pseudanomala* Norrbom, new species**

(Figs. 2J, 8D, 9D, 10H)

Anastrepha anomala: Stone 1942: 29 [in part].

Recognition.—*Anastrepha pseudanomala* is one of the species of the *serpentina* group with a hyaline area in cell br posterior to the pterostigma that is not extended to vein R_{4+5}. Of the other species with this character, *A. pseudanomala* is most likely to be confused with *A. normalis* or *A. anomala.* It differs from both species in having a slightly longer aculeus tip (more than 0.35 mm long) that is broader than in *A. anomala* (0.15 mm vs. no more than 0.12 mm), and more than half serrate, unlike in *A. normalis.* The orbital plate sometimes has a triangular brown mark that does not occur in the other two species. *A. pseudanomala* further differs from *A. normalis* in having the middle section of the S-band solidly dark brown anterior and distal to crossvein R-M.

Description.—Largely dark orange to dark red brown with yellow markings. Setae dark brown. *Head:* Mostly yellow. Ocellar tubercle brown. Orbital plate with paired, faint to moderate brown, triangular spot. Facial carina, in profile, concave. 3–4 frontal setae; 1–2 orbital setae, posterior seta well developed if present. Ocellar seta weak, short to minute. Antenna extended 0.80–0.85 distance to lower facial margin. *Thorax:* Mostly orange to dark red brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally only slightly beyond level of acrostichal seta (at most one third distance to level of dorsocentral seta); sublateral vitta extended from transverse suture to or almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area well separated from basal seta); propleuron; dorsal margin and anteroventral corner of anepisternum; all or most of greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal pattern similar to *A. normalis* (see Fig. 1B); broad area bordering medial vitta, shorter and narrower area bordering mesal margin of sublateral vitta, and large sublateral presutural area orange. Most of darker areas of anepisternum, anepimeron, meron, and katatergite dark brown. Katepisternum mostly orange. Subscutellum and mediotergite dark brown, narrowly dark orange medially. Mesonotum 3.62–3.70 mm long. Scutum microtrichose except for broad presutural bare area extended more than ⅔ distance to transverse suture; setulae mostly yellow, brown on parts of darker areas. Katepisternal seta weak, much shorter than postocellar seta, yellowish. *Wing* (Fig. 2J): Length 7.57–7.74 mm. Vein M strongly curved apically; section between BM-Cu and R-M 2.25–2.32 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.73–0.75 times as long as DM-Cu. Crossvein DM-Cu oblique, with anterior end more distal than posterior end. Pattern mostly dark brown. C-band and S-band broadly connected in cells r_{2+3} and br, but separated basally by hyaline area in posterior half of br aligned with pterostigma, hyaline basal sixth of cell dm, and hyaline to yellowish area covering all of cell bm. C-band yellowish to subhyaline in cell bc and posterior half to ⅔ of cell c; and with large yellow area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally to level of apex of vein R_1. S-band with large yellow area in cell dm extending slightly into cell br and nearly touching crossvein R-M; rest of band dark brown, including areas distal to and anterior to R-M; distal section slightly narrowed, at apex of vein R_{2+3} 0.47–0.49 times width of cell r_{2+3}; not extended to apex of vein M. Hyaline spot in cell r_1 nearly triangular, interrupted at or absent posterior to vein R_{2+3} and not extended to vein R_{4+5}; its apex aligned slightly basal to R-M. V-band with distal arm absent; proximal arm separated from S-band, extended narrowly to vein R_{4+5}; extended basally along posterior wing margin almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen:* Orange with yellow and brown markings. Syntergite 1+2 with band, brown laterally, orange medially; posterior margin broadly yellow, narrowing laterally. Tergite 3 and sometimes tergite 4 with basal bands, broad and brown laterally, paler and narrower medially; posterior margin narrowly yellow on medial ¾. Tergites 5–6 orange. *Male terminalia:* unknown. *Female terminalia:* Oviscape 4.12–4.28 mm long, 1.11–1.18 times as long as mesonotum. Eversible membrane (Fig. 8D) with 35–40 large, hook-like dorsobasal scales in triangular pattern. Aculeus 4.16 mm long; tip (Figs. 9D, 10H) 0.37–0.40 mm long, 0.15 mm wide, parallel-sided basally, apical 0.62–0.63 gradually tapered and very finely serrate. Spermathecae ovoid.

Distribution.—*Anastrepha pseudanomala* is known from Costa Rica and Panama.

Comments.—The terminalia were dissected only in the paratype, although the aculeus tip is exposed in the holotype.

Etymology.—The name of this species is based on its similarity to *A. anomala.*

Biology.—The host plants of this species are unknown.

Type data.—Holotype ♀ (USNM52961), PANAMA: Panamá: El Cermeño [8°44′N 79°51′W], 10 Oct 1939, J. Zetek 4559, paratype *A. anomala.* Paratype ♀ (USU USNM50455), COSTA RICA: Alajuela: 20 km. S of Upala, 30 Oct 1990, F. D. Parker.

Anastrepha pulchella Norrbom, new species

(Figs. 1E, 3A, 10I)

Anastrepha pulchra: Stone 1942: 26 [in part], Plate 2C.

Recognition.—*Anastrepha pulchella* differs from all other species of *Anastrepha* in having a second hyaline area in cell r_1, between the S-band and vein R_{2+3}. It is one of three species of the *serpentina* group with the C- and S-bands broadly fused so that there is no hyaline area in the middle of cell br. It differs from the other two species, *A. pulchra* and *anomoiae,* in having the aculeus tip shorter (less than 0.30 mm long) and more than half serrate, the scutum with narrow orange dorsocentral vittae that are broad and fan-shaped anteriorly, the S-band meeting costa in cell r_1 at a sharp angle, so that the basal marginal hyaline spot in cell r_1 is triangular, and the apex of the basal hyaline spot in cell r_1 is aligned proximal to crossvein R-M. See diagnoses of *A. pulchra* and *anomoiae* for additional differences.

Description.—Largely dark orange to dark red brown with yellow markings. Setae dark brown. *Head:* Mostly yellow. Ocellar tubercle brown. Occiput with small paired dorsal brown spot in one female. Facial carina, in profile, concave. 4–5 frontal setae; 2 orbital setae, posterior seta well developed. Ocellar seta weak, small to minute. Antenna extended 0.75–0.85 distance to lower facial margin. *Thorax* (Fig. 1E): Mostly orange brown to red brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally only slightly beyond level of acrostichal seta (at most half distance to level of dorsocentral seta); sublateral vitta extended from transverse suture to or almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area well separated from basal seta); dorsal margin of anepisternum; greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal darker areas mostly red brown to dark brown, sometimes with narrow area bordering medial vitta, shorter narrow area bordering mesal margin of sublateral vitta, or small sublateral presutural area orange; with narrow orange vitta on dorsocentral line, its anterior end expanded laterally, somewhat fan-shaped. Most of darker areas of anepisternum, anepimeron, meron, and katatergite dark brown. Katepisternum mostly orange or partly brown. Subscutellum and mediotergite dark brown, usually narrowly orange medially. Mesonotum 3.33–3.74 mm long. Scutum microtrichose except for broad medial anterior area extended ¾ distance to transverse suture; setulae mostly yellow, but brown on parts of dark areas. Katepisternal seta weak, shorter than postocellar seta, yellowish to red brown. *Wing* (Fig. 3A): Length 7.24–8.07 mm. Vein M strongly curved apically; section between BM-Cu and R-M 3.58–4.22 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.49–0.58 times as long as DM-Cu. Crossvein DM-Cu slightly oblique, with anterior end more distal than posterior end. Pattern mostly dark brown. Basally with large infuscated area formed by fusion of C-band and base of S-band, which are separated only by hyaline to yellowish area covering cell bm and basal seventh or less of cell dm; basal area mostly brown, but cell bc and cell c except anterior margin yellowish to subhyaline, cell sc yellow including base or sometimes most of pterostigma, and cell r_1 with small yellow area extending no more than ⅓ length of pterostigma; most of cell bcu except lobe, and small basal area in cell cu_1 also yellow; cell r_{2+3} basal to level of apex of vein R_1 and all of cell br infuscated, brown except br often partially yellow basal to BM-Cu. Remainder of S-band brown except sometimes partially orange in cell r_1; distal section slender, at apex of vein R_{2+3} 0.31–0.43 times width of cell r_{2+3}; not closely following vein R_{2+3} so that basal marginal hyaline spot in cell r_1 at most slightly elongate along costa, nearly triangular, and second hyaline spot present in r_1 between band and vein R_{2+3}; not extended to apex of vein M. Hyaline marginal spot in cell r_1 sometimes interrupted at vein R_{2+3}, sometimes extended almost to vein R_{4+5}; its apex aligned slightly basal to R-M. V-band with distal arm absent; proximal arm slender, extended to vein R_{4+5}, usually separated from S-band, narrowly connected to S-band along R_{4+5} in one female; extended basally along posterior wing margin to or almost to vein A_1+Cu_2 where sometimes connected to extension from base of S-band. *Abdomen* (Fig. 1E): Banded with yellow, orange and dark brown. Syntergite 1+2 and tergites 3 and 4 each with brown band only slightly and very gradually narrower medially; posterior margin yellow, narrowing laterally. Tergite 5 and female tergite 6 orange. *Male terminalia:* Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view very slightly curved; in posterior view, with small to moderate basolateral lobe, main part triangular, acute apically. Proctiger with lateral fold separating sclerotized areas. Phallus 5.62–5.70 mm long; 1.65–1.69 times as long as mesonotum. Glans 0.55–0.60 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 4.58–4.91 mm long, 1.29–1.31 times as long as mesonotum. Eversible membrane not everted in the dissected specimens, with perhaps 35 large, hook-like dorsobasal scales in triangular pattern. Aculeus 4.60–4.91 mm long; base expanded; tip (Fig. 10I) 0.24–0.26 mm long, 0.15–0.16 mm wide, distal 0.62–0.65 serrate. Spermathecae pear shaped.

Distribution.—*Anastrepha pulchella* is known only from Panama.

Biology.—The host plants of this species are unknown.

Etymology.—The name of this species is a Latin adjective meaning beautiful. It was also chosen because of the similarity of this species and *A. pulchra,* whose name is derived from the same root.

Type data.—Holotype ♀ (USNM51717), PANAMA: Panamá: El Cermeño [8°44′N 79°51′W], 17 Oct 1939, J. Zetek 4566, paratype *A. pulchra.* Paratypes: PANAMA: Panamá: Arraijan [8°57′N 79°39′W], May 1949, J. Zetek 5405, 1 ♀ (USNM52978); Barro Colorado Island [9°9′17″N 79°50′53″W], Sep 1943, J. Zetek 5101, 1 ♀ (USNM52982); El Cermeño, 19 Dec 1939, J. Zetek 4602, 1 ♂ (USNM52989); La Campana [8°43′N 79°54′W], Muñoz Grove, 7 Dec 1938, J. Zetek 4298, 1 ♀ paratype *A. pulchra* (USNM52972).

Anastrepha pulchra Stone
(Figs. 1F, 3B–C, 6C–D, 10J)

Anastrepha pulchra Stone 1942: 26 [description]; Foote 1967: 15 [in catalog]; Steyskal 1977: 8 [in key]; Caraballo 1981: 50 [Venezuela, host]; Norrbom and Kim 1988: 51 [host list]; Norrbom et al. 1999a: 81 [in catalog]; Norrbom, in press [host database].

Recognition.—*Anastrepha pulchra* is one of three species of the *serpentina* group with the C- and S-bands broadly fused so that there is no hyaline area in the middle of cell br. It differs from the other two species, *A. pulchella* and *anomoiae,* in having a triangular brown mark on the orbital plate, and narrower, more elongate, yellow medial areas on the posterior margins of abdominal tergites 3 and 4, and in the male, cells bm and dm entirely infuscated. The aculeus tip is 0.33–0.46 long (shorter than in *A. anomoiae,* longer than in *A. pulchella*), and entirely nonserrate. The marginal hyaline spot in cell r_1 is elongated along the costa, and its apex is aligned with or distal to crossvein R-M; it is aligned with R-M in *A. anomoiae* and proximal to it in *A. pulchella.* See diagnoses of *A. pulchella* and *anomoiae* for additional differences.

Description.—Largely dark orange to dark red brown with yellow markings. Setae dark brown. *Head:* Mostly yellow. Ocellar tubercle and paired triangular area on orbital plate brown. Occiput with paired, triangular or comma-shaped, brown mark covering suture of median occipital sclerite. Facial carina, in profile, concave. 3–5 frontal setae; 1–2 orbital setae, posterior seta well developed if present. Ocellar seta weak, small to minute. Antenna extended 0.75–0.85 distance to lower facial margin. *Thorax* (Fig. 1F): Mostly orange brown to red brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally only to or slightly beyond level of acrostichal seta (at most one fourth distance to level of dorsocentral seta); sublateral vitta extended from transverse suture almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area well separated from basal seta); dorsal margin of anepisternum; dorsal half to all of greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal darker areas mostly red brown to dark brown, sometimes with narrow area bordering medial vitta, shorter narrow area bordering mesal margin of sublateral vitta, or small sublateral presutural area orange; without orange vitta on dorsocentral line. Most of darker areas of anepisternum, anepimeron, meron, and katatergite dark brown. Katepisternum mostly orange or partly brown. Subscutellum and mediotergite dark brown, usually narrowly orange medially. Mesonotum 3.04–4.08 mm long. Scutum microtrichose except for broad medial anterior area extended ⅓–⅔ distance to transverse suture; setulae mostly brown, but yellow on vittae and in broad band across middle of presutural area. Katepisternal seta weak, at most as long as postocellar seta, yellowish. *Wing* (Figs. 3B–C): Length 6.17–8.89 mm. Vein M strongly curved apically; section between BM-Cu and R-M usually 3.05–3.64 times as long as section between R-M and DM-Cu, 4.18–4.75 in 2 Venezuelan males; section between R-M and DM-Cu usually 0.58–0.71 times as long as DM-Cu, 0.48–0.51 in 2 Venezuelan males. Crossvein DM-Cu slightly to distinctly oblique, with anterior end more distal than posterior end. Pattern mostly dark brown. Basally with large infuscated area formed by fusion of C-band and base of S-band, which are separated in female only by hyaline to yellowish area covering most of cell bm and basal eighth or less of cell dm, in male cells bm and dm entirely infuscated although cell bm sometimes paler anteriorly; basal area mostly brown, but cell bc, cell c except anterior margin, and much of basal part of cell bcu yellow to subhyaline in female, these areas darker or smaller in male; often much of pterostigma, sometimes small area in cells sc and r_1 posterior to bend in vein Sc also yellow or paler brown; cell r_{2+3} basal to level of apex of vein R_1 and all of cell br brown. Remainder of S-band brown except sometimes partially orange in cell r_1 bordering costa; distal section slender, at apex of vein R_{2+3} 0.26–0.38 times width of cell r_{2+3}; closely following vein R_{2+3} so that basal marginal hyaline spot in cell r_1 elongate along costa; not extended to apex of vein M. Hyaline marginal spot in cell r_1 extended to vein R_{4+5}; its apex aligned with R-M or slightly distal to it. V-band with distal arm absent; proximal arm slender, often extended to vein R_{4+5} but usually fainter or absent in anterior half to ⅔ of cell r_{4+5}, separated from S-band; extended basally along posterior wing margin almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen* (Fig. 1F): Predominantly brown with yellow and orange areas sometimes almost forming T-shaped pattern, especially in male. Syntergite 1+2 mostly brown, with broad medial area and posterior margin broadly yellow; tergites 3 and 4 each with brown band distinctly narrower medially, sometimes interrupted on tergite 4; posterior margin with more elongate, narrower (less than half width of tergite), often trapezoidal yellow area. Tergite 5 brown laterally, yellow to orange medially. Female tergite 6 orange. *Male terminalia* (Figs. 6C–D): Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view very slightly curved; in posterior view without strong basolateral lobe, main part narrowly triangular, acute apically. Proctiger with lateral fold separating sclerotized areas. Phallus 5.45–6.24 mm long; 1.77–1.90 times as long as mesonotum. Glans 0.55–0.60 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 4.28–5.74 mm long, 1.25–1.41 times as long as mesonotum. Eversible membrane with 35–55 large, hook-like dorsobasal scales in triangular pattern. Aculeus 4.00–5.70 mm long; base expanded; tip (Fig. 10J) 0.33–0.46 mm long, 0.14–0.16 mm wide, nonserrate, tapered rapidly subbasally (slightly less so in Venezuela female examined), then gradually to broad, blunt apex. Spermathecae pear shaped.

Distribution.—*Anastrepha pulchra* is known from Panama, Venezuela (Aragua and Bolivar), and Brazil (Amazonas).

Biology.—The only reported host plant is an undetermined species of Sapotaceae (Caraballo 1981).

Comments.—The wing illustration in Stone (1942, Pl. 2C) is of *A. pulchella.* The two males examined from Venezuela have the section of vein M between R-M and DM-Cu short, but the females are within the range of the other specimens for this character. The aculeus tip of the single Venezuelan female dissected has the tip slightly less tapered basally than in other females. The Brazilian female has the longest aculeus tip, although it is among the shortest in oviscape and aculeus length.

Type data.—Holotype ♀ (USNM52984), PANAMA: Panamá: La Campana, 2 May 1939, J. Zetek 4361 [examined].

Other specimen data.—BRAZIL: Amazonas: Manaus, Campus Univ., 27 Jan 1973, J.A. Rafael, 1 ♀ (INPA USNM52971). PANAMA: Panamá: Arraijan, 24 Jul 1947, J. Zetek 5290, 1 ♂ (USNM52976); same, 5 Jun 1947, J. Zetek 5283, 1 ♀ (USNM52977); same, 18 May 1950, J. Zetek 5460, 1 ♀ (USNM52979); same, 23 Jun 1949, J. Zetek 5411, 1 ♀ (USNM52980); same, 25 May 1950, J. Zetek 5461, 1 ♂ (USNM52981); same, 29 May 1947, J. Zetek 5282, 1 ♀ (USNM52988); Balboa Bay, 17 Mar 1952, E.E. Hooser, 1 ♂ (USNM52983); El Cermeño [8°44′N 79°51′W], 5 May 1942, J. Zetek 4939, 1 ♀ (USNM51714); same, 9 Jun 1942, J. Zetek 4954, 1 ♀ (USNM51715); same, 20 May 1941, J. Zetek 4786, 1 ♀ (USNM51716); same, 12 May 1942, J. Zetek 4941, 1 ♂ (USNM51713); same, 16 May 1939, J. Zetek 4886, 1 ♀ (TAMU USNM52962); La Campana, 5 Jun 1939, J. Zetek 4433, 1 ♀ paratype (USNM52973); same, 30 May 1939, J. Zetek 4422, 1 ♀ paratype (USNM52974); same, 16 May 1939, J. Zetek 4397, 1 ♀ paratype (USNM52975). VENEZUELA: Bolívar: El Dorado—Santa Elena, Km. 38, 160 m, ex frutos de Sapotaceae, 2 Sep 1957, F. Fernandez Y. & C.J. Rosales, 2 ♂, 2 ♀ (USNM52967–70).

Anastrepha serpentina (Wiedemann)
(Figs. 1G, 3D–E, 7A–D, 11B)

Dacus serpentinus Wiedemann 1830: 521 [description]; Schiner 1868: 263 [as type species of *Anastrepha*]; Loew 1873: 227 [type data].

Leptoxys serpentina: Macquart 1843: 373 [classification].

Urophora vittithorax Macquart 1851: 259 [description]; Loew 1873: 227 [synonymy].

Trypeta serpentina: Loew 1873: 226 [classification].

Acrotoxa serpentina: Loew 1873: 227 [classification].

Anastrepha serpentina: Schiner 1868: 263 [classification]; Bezzi 1909: 283 [in catalog and key]; Hendel 1914: 14 [in key]; Greene 1929: 497 [larva, pupa]; Dampf 1933: 254, 260 [taxonomy, Mexico]; Emmart 1933: 184 [egg]; Lima 1934: 494 [taxonomy, hosts]; Greene 1934: 142 [revision]; Stone 1942: 27 [revision]; Baker et al. 1944: 115, 125 [larva, taxonomy, hosts, Mexico]; Phillips 1946: 33, 107 [larva, host list]; Aczél 1950: 227 [in catalog]; Bush 1962: 95 [karyotype]; Foote 1965: 673 [in catalog]; Foote 1967: 16 [in catalog]; Weems 1969: 1 [review]; Korytkowski and Ojeda 1968: 49 [Peru]; Wasbauer 1972: 107 [host list]; Steyskal 1977: 8 [in key]; Zucchi 1978: 80 [Brazil]; Berg 1979: 23 [in larval key]; Morgante et al. 1980: 623 [isozymes]; Caraballo 1981: 52 [Venezuela, hosts]; Norrbom and Kim 1988: 55 [host list]; Steck et al. 1990: 344 [in larval key]; Solferini and Morgante 1987: 236, 1990: 201 [karyotype]; Hernández-Ortiz 1992: 89 [Mexico]; White and Elson-Harris 1992: 152 [taxonomy, pest status, larva]; Matioli et al. 1992: 35 [isozymes]; Foote et al. 1993: 105 [taxonomy]; Selivon and Perondini 1999: 350 [egg]; Norrbom et al. 1999a: 82 [in catalog]; Norrbom, in press [host database].

Anastrepha serfentinus Foote 1965: 673 [misspelling].

Recognition.—*Anastrepha serpentina* is one of the species of the *serpentina* group with a hyaline area in cell br posterior to the pterostigma that is not extended to vein R_{4+5}. It differs from the other species with this character in having the abdomen mostly brown with a T-shaped medial yellow area and the distal section of the S-band slender, at apex of vein R_{2+3} less than 0.45 times width of cell r_{2+3}. Within the *serpentina* group, a similar abdominal pattern occurs only in *A. pulchra,* and elsewhere in *Anastrepha,* only in *A. shannoni* of the *grandis* group and some species of the *daciformis* group, particularly *A. macrura* Hendel and *A. zucchii* Norrbom. Other useful diagnostic characters include: orbital plate sometimes with triangular brown mark; thorax mostly dark brown; wing bands mostly dark brown; C- and S-bands connected; distal arm of V-band absent; and aculeus tip 0.37–0.46 mm long, 0.14–0.17 mm wide, finely serrate on more than distal half (Fig. 11B).

Description.—Largely dark orange to dark brown with yellow markings. Setae dark brown. *Head:* Mostly yellow. Ocellar tubercle brown. Orbital plate often (on approx. ¾ of nonteneral specimens sampled) with paired triangular brown area; frons rarely red or red brown between these areas forming single large mark. Frons occasionally orange to pale red brown anteromedially. Occiput usually with paired, triangular or comma-shaped, brown mark near or covering suture of median occipital sclerite. Facial carina, in profile, concave. 3–6 frontal setae; 1–2 orbital setae (absent on both sides in 9, and on one side in 7, of 40 specimens sampled), posterior seta usually well developed if present. Ocellar seta weak, small to minute. Antenna extended 0.75–0.85 distance to lower facial margin. *Thorax* (Fig. 1G): Mostly orange brown to brown with following areas yellow and distinctly contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, but extended laterally only slightly beyond level of acrostichal seta (at most half distance to level of dorsocentral seta); sublateral vitta extended from transverse suture almost to posterior margin, including intra-alar seta; scutellum except extreme base (brown area usually well separated from basal seta, but sometimes narrowly separated); dorsal margin and anteroventral corner of anepisternum; dorsal half to all of greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal darker areas mostly red brown to dark brown, often with narrow orange area bordering medial vitta, and less commonly with small sublateral presutural orange area; without orange vitta on dorsocentral line. Most of darker areas of anepisternum, anepimeron, meron, and katatergite dark brown. Katepisternum usually orange anteriorly and ventrally, brown posteriorly. Subscutellum and mediotergite red brown to dark brown, sometimes narrowly orange medially. Mesonotum 2.76–3.91 mm long. Scutum microtrichose except for broad medial anterior area extended ½–¾ distance to transverse suture; setulae mostly yellow to pale brown, but darker brown on some brown areas. Katepisternal seta weak, at most as long as postocellar seta, yellowish. *Wing* (Figs. 3D–E): Length 6.00–8.56 mm. Vein M strongly curved apically; section between BM-Cu and R-M 1.93–2.55 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.68–0.82 times as long as DM-Cu. Crossvein DM-Cu distinctly oblique, with anterior end more distal than posterior end. Pattern mostly dark brown. C-band and S-band broadly connected in cells r_{2+3} and br, but separated basally by hyaline area in posterior half of br aligned with pterostigma, hyaline basal fourth to third of cell dm, and hyaline to yellowish area covering all of cell bm. C-band yellowish to subhyaline in cell bc and cell c except anterior margin; with large yellowish area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally to or almost to level of apex of vein R_1. S-band with large yellow area in cell dm often extending into cell br and sometimes nearly touching crossvein R-M; rest of band dark brown, including areas distal to and anterior to R-M; distal section slender, at apex of vein R_{2+3} 0.32–0.43 times width of cell r_{2+3}; closely following vein R_{2+3} so that basal marginal hyaline spot in cell r_1 usually elongate along costa; rarely extended to apex of vein M. Hyaline marginal spot in cell r_1 usually extended beyond vein R_{2+3} but not extended to vein R_{4+5}; its apex aligned with R-M or slightly basal to it. V-band with distal arm absent, very rarely with 1–2 faint spots in cells r_{4+5} or m; proximal arm slender, usually extended to vein R_{4+5} but often fainter in anterior half to ⅔ of cell r_{4+5}, separated from S-band; extended basally along posterior wing margin almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen* (Fig. 1G): Predominantly brown with yellow and orange areas forming T-shaped pattern. Syntergite 1+2 mostly brown, often orange basally, with narrow transverse medial area and posterior margin broadly yellow but not reaching lateral margin. Tergites 3 and 4 mostly brown, with narrow, parallel-sided or trapezoidal medial yellow area. Tergite 5 mostly brown, with yellow to orange medial area larger than on tergite 4. Female tergite 6 orange. *Male terminalia* (Figs. 7A–D): Dorsal posterior margin of epandrium evenly convex. Lateral surstylus moderately long; in lateral view slightly curved; in posterior view usually with small basolateral lobe, main part triangular, acute apically. Proctiger with lateral fold separating sclerotized areas. Phallus 3.71–4.84 mm long; 1.15–1.40 times as long as mesonotum. Glans 0.55–0.60 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 2.58–3.91 mm long, 0.79–1.02 times as long as mesonotum. Eversible membrane with 55–65 large, hook-like dorsobasal scales in triangular pattern. Aculeus 2.58–3.83 mm long; base expanded; tip (Fig. 11B) 0.37–0.46 mm long, 0.14–0.17 mm wide, gradually tapered, apical 0.55–0.65 finely serrate. Spermathecae globose to ovoid.

Distribution.—*Anastrepha serpentina* is one of the most widely distributed species of *Anastrepha*. It occurs from northern Mexico south to Peru and Argentina, and is also known from Trinidad and Tobago and Curacao. There are sporadic trap records from southern Texas (USA) (e.g., 8 specimens in the Rio Grande Valley during 1995–98), but it is questionable whether *A. serpentina* has breeding populations there (D. B. Thomas, personal communication).

Biology.—*Anastrepha serpentina* is an

important pest in the American tropics and subtropics, especially of sapotaceous fruits, although it has also been reported to attack mango, several species of *Citrus,* apple, peach and quince. The reported field hosts include 45 species belonging to 28 genera and 17 families. Of the 18 genera and 29 species that are native hosts, five genera (including *Chrysophyllum, Manilkara, Micropholis, Pouteria,* and *Sideroxylon*) and 15 species belong to the Sapotaceae. See Norrbom (in press) for complete host data.

Type data.—*Dacus serpentinus:* Lectotype [here designated to fix and stabilize the current concept of the name] ♂ (NMW), Brazil. Wiedemann's extensive description of the wing and abdominal patterns leaves little doubt about the identity of this species. He did not state the number of specimens he examined, thus any putative type specimens should be regarded as syntypes. He did indicate that his specimens were female, from Brazil, and deposited in his collection, which was later sold to Winthem and then to the NMW. Loew (1873: 227) examined what he called "Wiedemann's original specimen", but did not mention its sex. Stone (1942) stated that there was a female holotype in the NMW, apparently based on Wiedemann's and Loew's statements; he did not examine this purported specimen or otherwise confirm its existence.

There appear to be no extant female syntypes of *serpentinus* in the NMW, but two males there and a third sent to the USNM in an exchange probably were Wiedemann specimens. The USNM male has labels with "69," "Dacus serpentinus Wied," "Brasilia Coll. Winthem," "Type" (red), "Cotype No. 51251 U.S.N.M." (orange), "This specimen is one of the original 3 types of Wiedemann," and "From Vienna Museum in exchange 1935 C.T.G." The latter two are in C.T. Greene's writing. One of the NMW males has a slightly greenish label with "serpentinus Wied. Brasil" in Wiedemann's writing and a label with "serpentinus Coll. Wiedem." The second male has labels with "Brasilia," "serpentinus Coll. Winthem," "Dacus serpentinus Wied Brasilia," and "serpentinus det. Löw." The writing on the latter two labels somewhat resembles the upper sample of Loew's labels in Horne and Kahle (1935–37). Presumably this is the specimen he examined. The "Coll. Winthem" and "Coll. Wiedem." labels were added when these collections were incorporated into the NMW. The "Brasilia" label on the NMW male and the determination label on the USNM male appear to be in the same writing.

The labels on the above specimens, especially the determination label in Wiedemann's writing, suggest that his statement about the sex of the types was erroneous, or that he at least had some male specimens. The former is supported by the fact that although his description of *serpentinus* was fairly extensive, he did not mention the "Legegrissel" or "Grissel," his name for the ovipositor, as he did in most descriptions of tephritid species under *Trypeta* or *Dacus* that were based on female specimens. He also said that the length was 3.5 lines (approximately 7.3 mm), which is extremely small for a female of *serpentina* when the ovipositor is included in the overall length as Wiedemann did (e.g., see his description of *Dacus parallelus,* 1830: 515). The three putative syntype males are, however, approximately this length, 7.5 mm long. Based on this information, I am assuming that the statement of the type sex in the original description was an error, and I have designated the male in the NMW with the Wiedemann determination label and the "Coll. Wiedem." label as lectotype. Besides having his label, of the three specimens, this male also most closely fits Wiedemann's description in having the first abdominal tergite (syntergite 1+2) yellow posteriorly; the margin is discolored by underlying tissues in the other two males.

Urophora vittithorax: Lectotype [here designated to fix and stabilize the current concept of the name] ♀ (UMO), "l'Inde" [India; error, possibly Trinidad]. Macquart described this species from an unstated number of female specimens belonging to Bigot. In the Bigot Collection (UMO) there is a female of *A. serpentina* with a label with "Urophora vittithorax [female symbol] Macq. n. sp." in Macquart's writing and "Oxyna (Bigot)" in Collin's writing, glued to a Bigot drawer label with "♀ D. Ex. nom" [= named in Dipteres Exotiques] in Bigot's writing. Except for missing one wing, the specimen is in good condition and is here designated as lectotype. Loew (1873) correctly guessed the identity of this species from Macquart's extensive description and accurate wing illustration (Tab. 26, fig. 11). As Loew noted, India, the type locality given by Macquart, is incorrect, but possibly refers to the West Indies; this species is endemic to the New World, and does occur in Trinidad and Curacao. Stone (1942) referred to the "holotype" in the Bigot Collection, but did not examine the specimen, so I do not consider his statement a lectotype designation by inference of holotype.

Anastrepha striata Schiner
(Figs. 1H, 3F–H, 7E–F, 11C–D)

Dictya cancellaria Fabricius 1805: 328; Hendel 1914: 83 [in catalog, as unrecognized species]; Zimsen 1964: 494 [type data]; Foote 1967: 58 [in catalog, as unplaced Tephritidae]; Knutson et al. 1976: 14 [erroneous synonymy]; Norrbom et al. 1999a: 82 [synonymy]. *Nomen oblitum.*

Anastrepha striata Schiner 1868: 264 [description]; Bezzi 1909: 283 [in catalog and key]; Hendel 1914: 19 [taxonomy; Peru, Bolivia]; Keilin and Picado 1920: 423 [larva, host, Costa Rica]; Greene 1929: 497 [larva, pupa]; Emmart 1933: 184 [egg]; Dampf 1933: 254, 260 [taxonomy, Mexico]; Lima 1934: 504 [taxonomy, Brazil]; Greene 1934: 145 [taxonomy]; Stone 1942: 29 [revision]; Baker et al. 1944: 130 [larva, taxonomy, hosts, Mexico]; Phillips 1946: 107 [host list]; Aczél 1949: 229 [in catalog]; Bush 1962: 94 [karyotype]; Foote 1965: 673 [in catalog], 1967: 16 [in catalog]; Hardy 1968: 136 [type data]; Korytkowski and Ojeda 1968: 50 [Peru]; Wasbauer 1972: 108 [host list]; Steyskal 1977: 5 [in key]; Zucchi 1978: 85 [Brazil]; Zucchi 1979: 265 [type data, taxonomy]; Morgante et al. 1980: 623 [isozymes]; Caraballo 1981: 62 [Venezuela, hosts]; Weems 1982: 1 [review]; Norrbom and Kim 1988: 62 [host list]; Solferini and Morgante 1987: 238, 1990: 202 [karyotype]; Steck et al. 1990: 343 [in larval key]; Steck 1991: 11 [isozymes]; Hernández-Ortiz 1992: 85 [Mexico]; White and Elson-Harris 1992: 155 [taxonomy, pest status, larva]; Matioli et al. 1992: 35 [isozymes]; Foote et al. 1993: 108 [taxonomy]; Norrbom et al. 1999a: 82 [in catalog]; Malavasi and Zucchi 2000 [Brazil]; Norrbom, in press [host database].

Recognition.—*Anastrepha striata* differs from all other species of *Anastrepha* except *A. bistrigata* in having the dorsal posterior margin of the epandrium with a narrow, V-shaped, medial indentation, and by the following combination of characters: mesonotum with large, somewhat U-shaped, brown area, often interrupted at transverse suture, but without other brown markings; mediotergite and subscutellum entirely brown or at least brown laterally; thoracic pleuron and abdomen without brown areas; and scutum microtrichose, with broad nonmicrotrichose stripe, sometimes interrupted at transverse suture, on dorsocentral line. These two species share additional characters, including: wing bands, particularly middle section of S-band, mostly orange brown; cell br with hyaline area posterior to pterostigma extending width of cell, reaching vein R_{4+5}; aculeus tip broad, at least 0.17 mm wide, and bluntly triangular; and lateral surstylus with rounded subapical lateral lobe. *Anastrepha striata* differs from *A. bistrigata* as indicated in the key and also in having a shorter aculeus tip (0.24–0.31 vs. 0.35–0.40 mm) and a slightly longer and narrower lateral surstylus that is more or less parallel to the opposite surstylus. The scutal microtrichia are usually denser and whiter in appearance in oblique anterior view than in *A. bistrigata,* and the wing bands are usually slightly paler.

Description.—Largely orange with dark brown and yellow markings. Setae red-brown to dark brown. *Head:* Yellow except ocellar tubercle brown. Facial carina, in profile, concave. 3–6, usually 4–5, frontal setae; 2 or rarely 1 orbital setae (posterior seta absent on one side in 2 of 25 specimens sampled), posterior seta well developed. Ocellar seta weak and small or minute. Antenna extended 0.70–0.85 distance to lower facial margin. *Thorax* (Fig. 1H): Mostly orange with following areas yellow and often contrasting: postpronotal lobe; single medial and paired sublateral vittae on scutum, the slender medial vitta extended nearly full length of scutum, broadened posteriorly, extended laterally half to ¾ distance from level of acrostichal seta to that of dorsocentral seta; sublateral vitta extended from transverse suture almost to posterior margin, including intra-alar seta; scutellum except extreme base of disc (brown area well separated from basal seta); propleuron; dorsal margin of anepisternum; dorsal half of greater ampulla; dorsal margin of katepisternum; katepimeron; and most of anatergite and katatergite. Mesonotal pattern with following orange areas: broad area bordering medial vitta, usually small sublateral presutural area, usually narrow area bordering mesal margin of sublateral vitta, and area lateral to sublateral vitta except extreme posterior margin. Dark brown, somewhat U-shaped mark narrowed or usually interrupted at or anterior to transverse suture. Darker areas of pleuron orange. Subscutellum and mediotergite dark brown, narrowly to broadly orange medially. Mesonotum 2.91–3.41 mm long. Scutum with microtrichia relatively dense giving white appearance when viewed from oblique anterior angle; with short medial presutural bare area sometimes (Brazilian and Bolivian specimens examined) extended narrowly along medial vitta as far as transverse suture; always with broad nonmicrotrichose areas on parts of dark brown marks, 1 presutural, 1 postsutural between medial and sublateral vittae and extended to or almost to level of dorsocentral seta; these areas usually well separated at transverse suture, but rarely narrowly connected (one female, Huitanaã, Brazil, CMP, USNM53080); setulae usually strongly contrasting, whitish medially, dark brown on and lateral to nonmicrotrichose areas except for patch of white setulae on lateral part of presutural nonmicrotrichose area; brown setulae especially dense on nonmicrotrichose areas on brown marks and sparse to absent on narrow area lateral to postsutural nonmicrotrichose area. Katepisternal seta moderately developed, weaker than but longer than postocellar seta, pale to dark brown. *Wing* (Figs. 3F–H): Length 6.41–7.32 mm. Vein M strongly curved apically; section between BM-Cu and R-M 1.83–2.44 times as long as section between R-M and DM-Cu; section between R-M and DM-Cu 0.75–0.91 times as long as DM-Cu. Crossvein DM-Cu oblique, with anterior end more distal than posterior end. Pattern mostly yellow to orange brown and moderate brown. C-band and S-band usually narrowly connected or separated, occasionally broadly connected, along vein R_{4+5}; often connected in cells r_1 and/or r_{2+3}; separated basally by hyaline area extending width of cell br and aligned with pterostigma, and covering basal seventh to fourth of cell dm and all of cell bm. C-band with cell bc and most of cell c yellowish, the latter sometimes subhyaline medially or darker anteriorly and basally; with large yellow area in base of cell sc and cells r_1 and r_{2+3} posterior to pterostigma, extending distally to or almost to level of apex of vein R_1; most of pterostigma, usually narrow distal margin, and base of cell br dark orange brown to moderate brown. S-band with middle section between costa and vein Cu_1 largely yellow to orange with narrow brown margins, darkening distally; distal section of band slightly narrowed to moderately broad, at apex of vein R_{2+3} 0.44–0.63 times width of cell r_{2+3}; separated from apex of vein M. Hyaline spot in cell r_1 nearly triangular, sometimes extended to vein R_{4+5}, but often interrupted in cell r_1 or r_{2+3} or absent in r_{2+3}; its apex aligned distinctly basal to R-M. V-band with distal arm usually complete and connected to proximal arm, but often fainter anteriorly, sometimes (especially in specimens from Guianas and northern Brazil) reduced or absent; proximal arm usually extended to vein R_{4+5}, often fainter in cell r_{4+5}; separated from S-band; extended basally along posterior wing margin almost to vein A_1+Cu_2 but not connected to extension from base of S-band. *Abdomen* (Fig. 1H): Mostly orange; posterior margins of tergites narrowly yellow, this area narrower laterally and also on successive tergites, nearly absent on tergite 5 and female tergite 6. *Male terminalia* (Figs. 7E–F): Dorsal posterior margin of epandrium with narrow, V-shaped, medial indentation. Lateral surstyli moderately long, parallel; each basally with narrow, posteriorly projecting ridge bordering medial surstylus; in lateral view slightly posteriorly curved, extreme apex with small but strong posterior projection; in posterior view without strong basolateral lobe, main part somewhat triangular, with rounded subapical lateral lobe. Proctiger with lateral fold separating sclerotized areas. Phallus 3.95–4.20 mm long; 1.27–1.37 times as long as mesonotum. Glans 0.45–0.50 mm long; acrophallus relatively stout. *Female terminalia:* Oviscape 2.32–2.66 mm long, 0.74–0.86 times as long as mesonotum (Fig. 1H). Eversible membrane with 50–60 large, hook-like dorsobasal scales in triangular pattern. Aculeus 1.97–2.25 mm long; tip (Figs. 11C–D) 0.24–0.31 mm long, 0.175–0.20 mm wide, nonserrate or with a few minute subapical serrations, broadly triangular and blunt apically. Spermathecae ovoid to pear-shaped.

Distribution.—Mexico (north to southern Sinaloa, Aguascalientes, and northern Veracruz) south to Bolivia and Brazil (Amazonas, Roraima, Rondonia, Pará, Amapá, Maranhão, Piauí, Mato Grosso do Sul, Goiás, São Paulo). Specimens are sporadically trapped in the United States (Foote et al. 1993), but those captured in California are clearly adventive and those taken in the Rio Grande Valley of southern Texas (including several specimens since 1995, D. B. Thomas, personal communication) questionably represent a breeding population.

Biology.—*Anastrepha striata* is an important pest in the American tropics and subtropics, especially of guavas and other myrtaceous fruits, although it has also been reported to attack mango, mombins, orange, and peach. The reported field hosts include 37 species belonging to 23 genera and 17 families. Of the 16 genera and 26 species that are native hosts, four genera (including *Campomanesia, Eugenia, Myrcia,* and *Psidium*) and 12 species belong to the Myrtaceae. See Norrbom (in press) for complete host data.

Type data.—*Dictya cancellaria:* Lectotype [here designated to fix and stabilize the current concept of the name] ♀ (UZMC), Guyana, Smidt. Fabricius described this nominal species from an unstated number of syntypes of unstated sex from "America meridionali" collected by Smidt. According to Zimsen (1964) and Papavero (1971: 21), the Fabrician specimens with this data originated from the West Indies or Guyana, the latter of which must be the type locality since this species is not known from the Antilles. There are two female syntypes in the UZMC collection, both with red "TYPE" labels, one of which (here designated as lectotype) is pinned through a handwritten label with "D. cancellaria, ex. Am. Mer. Schmidt." Both specimens are in good condition. They are unusual in having only one orbital seta, but otherwise fit the concept of this species. The hyaline spot in cell r_1 is small, and as in many specimens from the Guianas, the distal arm of the V-band is reduced (absent in cell r_{4+5}). The statements in the original description that the thorax is yellow with two interrupted black lines (Thorax . . . flavescens: lineis duabus antice interruptis, atris), the subscutellum and mediotergite have dark markings (Puncta duo atra sub scutello), and the abdomen and legs are yellow confirm that these specimens are authentic types and that the interpretation of this species as a synonym of *Ropalomera clavipes* (Fabricius) (Ropalomeridae) by Knutson et al. (1976) was erroneous.

Anastrepha striata: Lectotype ♀ (NMW), South America [Venezuela]; designated by inference of holotype by Hardy (1968: 136). Zucchi (1979) redescribed the lectotype and reported its label data.

Comments.—The mesonotal color pattern in this species is the most complex in *Anastrepha,* with strong contrast in all of the components (cuticle color, microtrichial pattern and density, and setulae color).

Norrbom et al. (1999a: 82) noted that the name *cancellaria* Fabricius has priority over *striata* Schiner, and that usage of the latter would require suspension of I.C.Z.N. rules. However, under the subsequently published fourth edition of the Code (Art. 23.9), *striata* is the valid name due to prevailing usage (*nomen protectum*), because to my knowledge, *cancellaria* has not been used as a valid name after 1899. The five uses of the name cited above in the synonymy are excluded under Art. 23.9.6. On the other hand, *striata* has been used as the name for this species in dozens, if not hundreds, of publications throughout the last century.

Anastrepha sp.
(Fig. 2E)

A single male examined from southern Mexico is similar to *A. anomala, normalis,* and *pseudanomala,* but its wing bands are mostly brown (unlike in *A. normalis*), the lateral surstylus is without a basolateral lobe (unlike in *A. anomala*), and the distal arm of the V-band is complete (unlike all three species). It probably represents a new species, but it is not formally described here because male terminalia are often not species specific in *Anastrepha,* and there is variation in the distal arm of the V-band in some species (e.g., *A. striata*).

Specimen data. MEXICO: Chiapas: Tapachula, 4 Aug 1956, W.E. Stone, 1 ♂ (USNM52942).

Phylogeny

Steyskal (1977) originally included *A. serpentina, pulchra, anomala, ocresia, ornata, fenestrata* (Lutz and Lima) and *phaeoptera* (Lima) in the *serpentina* group. The latter two species are now placed in the *robusta* species group (Norrbom et al. 1999b). Norrbom and Kim (1988) and Norrbom et al. (1999b) instead included *A. ornata* along with *A. striata* and *bistrigata* in the *striata* species group based on similar scutal microtrichial patterns and aculeus tip shape, although they suggested that the *serpentina* and *striata* groups might be closely related. As noted by Stone (1942), *A. ornata* resembles some species of the *serpentina* group (*sensu stricto*) in wing pattern and body color, but its terminalia are similar to *A. striata* and *bistrigata.*

Norrbom et al. (1999b) considered the *serpentina* group (*sensu stricto*) to be defined by several apomorphic character states. The most important was the bicolored, partially dark brown abdomen, although they noted that abdominal markings also occur in *A. ornata* and in a few species of the *cryptostrepha, schausi, punctata, grandis* and *daciformis* groups. Two other character states considered as possible synapomorphies were aculeus tip shape (long, moderately broad, evenly tapered, and partially finely serrate; this occurs in the previously included species except *A. pulchra*) and wing pattern relatively dark brown. Considering the additional variation discovered in aculeus tip shape in the new species described in this paper, and the paler color of the wing pattern in *A. normalis,* the latter two characters do not appear to be synapomorphies that define a restricted *serpentina* group.

Table 1. Useful taxonomic characters in the *serpentina* group. Only those preceeded by asterisk were used in the cladistic analysis.

1. Orbital plate and bordering areas—0) without brown markings; 1) orbital plate with triangular brown mark; 2) areas bordering orbital plate brown, or those areas and orbital plate brown.

*2. Color of darker areas of thorax and abdomen (areas exclusive of yellow vittae, bands and other markings)—0) yellow brown to orange; 1) mesonotum with brown markings and subscutellum and mediotergite mostly brown; 2) abdomen, mesonotum, subscutellum, mediotergite and thoracic pleuron with dark brown areas. State 0 occurs rarely in *A. ocresia,* but it was coded state 2, the usual state, in the analysis. [additive]

*3. Scutal microtrichia pattern—0) entirely microtrichose or with only medial presutural bare area; 1) with dorsocentral bare stripes; 2) bare except extreme lateral margin. [nonadditive]

4. Crossvein DM-Cu orientation—0) with anterior end distinctly more distal than posterior end; 1) with anterior end only slightly more distal or more basal than posterior end.

*5. Wing pattern color—0) bands largely orange brown with narrow brown margins; 1) bands mostly dark brown, S-band dark brown, including areas distal to and anterior to R-M.

*6. C-band and S-band basally—0) separated by hyaline area in cells bm, dm, and br, extending full width of latter in part posterior to pterostigma; 1) separated by hyaline area in cells bm, dm, and no more than posterior ⅔ of part of br posterior to pterostigma; 2) separated basally at most by hyaline area in cells bm and dm. [additive]

*7. C-band yellowish area in cells r_1 and r_{2+3} posterior to pterostigma—0) large, extending distally into cells r_1 and r_{2+3} at least to level of midlength of pterostigma; 1) small, not extending beyond cell r_1 nor distally beyond level of basal third of pterostigma.

8. Hyaline spot in cell r_1 between S-band and vein R_{2+3}—0) absent; 1) present.

*9. S-band, width of distal section oat apex of vein R_{2+3}/ width of cell r_{2+3}—0) 0.45–0.70; 1) less than 0.45; 2) greater than 0.70. The ratio varies from 0.53–1.00 in *A. ornata,* and is less than 0.45 in the Brazilian female of *A. anomala,* but the former was coded state 2 and the latter state 1 in the cladistic analysis because the S-band is broader more distally in the specimens with the lower ratios. [nonadditive]

10. S-band—0) not extended to apex of vein M; 1) extended to apex of vein M.

*11. Hyaline marginal spot in cell r_1 shape—0) nearly triangular; 1) distal side larger or elongated along costa; 2) connected to hyaline area in cell br. [nonadditive]

12. Hyaline marginal spot in cell r_1 alignment—0) apex aligned basal to R-M; 1) apex aligned with R-M; 2) apex aligned distal to R-M.

13. V-band distal arm—0) complete; 1) partially absent, present at least from vein M to margin; 2) absent, or rarely with small faint spot in cell m.

14. V-band proximal arm—0) extended along posterior wing margin but not connected to extension from base of S-band along vein A1+Cu2; 1) extended along posterior wing margin and connected to extension from base of S-band along vein A1+Cu2; 2) not extended along posterior wing margin.

15. V-band proximal arm—0) connected to S-band along vein R_{4+5}; 1) separated from S-band anteriorly; 2) connected to S-band near middle of crossvein R-M.

16. Abdominal tergite color—0) orange with posterior margins yellow; 1) at least syntergite 1+2 and tergite 3 with dark brown bands; 2) mostly brown with somewhat T-shaped yellow area.

*17. Dorsal, posterior margin of epandrium—0) evenly convex; 1) with narrow, V-shaped, medial indentation.

*18. Lateral surstylus mesal margin bordering medial surstylus—0) not projecting; 1) projecting posteriorly as narrow ridge.

*19. Lateral surstylus basolateral lobe—0) absent; 1) small to moderate; 2) strong. [nonadditive]

*20. Lateral surstylus in posterior view—0) triangular or tapering, without subapical, lateral lobe; 1) with rounded or truncate subapical lateral lobe.

*21. Aculeus tip shape—0) at least half serrate, gradually tapered or basal nonserrate part parallel-sided; 1) nonserrate, gradually tapered; 2) nonserrate or serrate only subapically, very broad and bluntly triangular; 3) nonserrate or serrate only subapically, rapidly tapered basally, then parallel sided until near apex. [nonadditive]

A reanalysis of the 11 species here included in the group was conducted based on the characters and character states indicated in Tables 1 and 2. Only the 12 characters indicated by an asterisk in Table 1 were used in the analysis; the others are either intraspecifically variable or are autapomorphies of individual species. The spe-

Table 2. Character state matrix for the species of the *serpentina* group. See Table 1 for explanation of character numbers. For intraspecifically variable characters, the predominant state is listed first. Parentheses indicate states that are rare.

	Character number																				
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
dissimilis		0	0		0	0	0	0	0		0						0	0	0	0	0
striata	0	1	1	0	0	0	0	0	0	0	0	0	0–2	0	1	0	1	1	0	1	2
bistrigata	0	1	1	0	0	0	0	0	1	0	0	0	0, 1	0	1	0	1	1	0	1	2
ornata	0, 2	2	1	0	1	1	0	0	0, 2	1, 0	2	?	2	1	1	1	0	0	0	1	2
normalis	0	2	0	0	0	1	0	0	0	0, 1	0	0	2	0	1, 0	1	0	0	0	0	1
ocresia	0	2 (0)	2	0	1	1	0	0	2	1, 0	0	0	1	0	1, 0	1	0	0	2	0	0
anomala	0	2	0	0	1	1	0	0	0, 1	0	0	0, 1	2	0	1	1	0	0	2	0	0
pseudanomala	0, 1	2	0	0	1	1	0	0	0	0	0	0	2	0	1	1	?	?	?	?	0
sp. (Mexico)	0	2	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	?
serpentina	0, 1	2	0	0	1	1	0	0	1	0 (1)	1	0, 1	2	0	1	2	0	0	1	0	0
pulchella	0	2	0	0, 1	1	2	1	1	1	0	0	0	2	0, 1	1 (0)	1	0	0	1	0	0
pulchra	1	2	0	0, 1	1	2	1	0	1	0	1	1, 2	2	0	1	1, 2	0	0	0	0	3
anomoiae	0	2	0	1	1	2	1	0	1	0	1	1	2	2	2	1	0	0	1	0	3

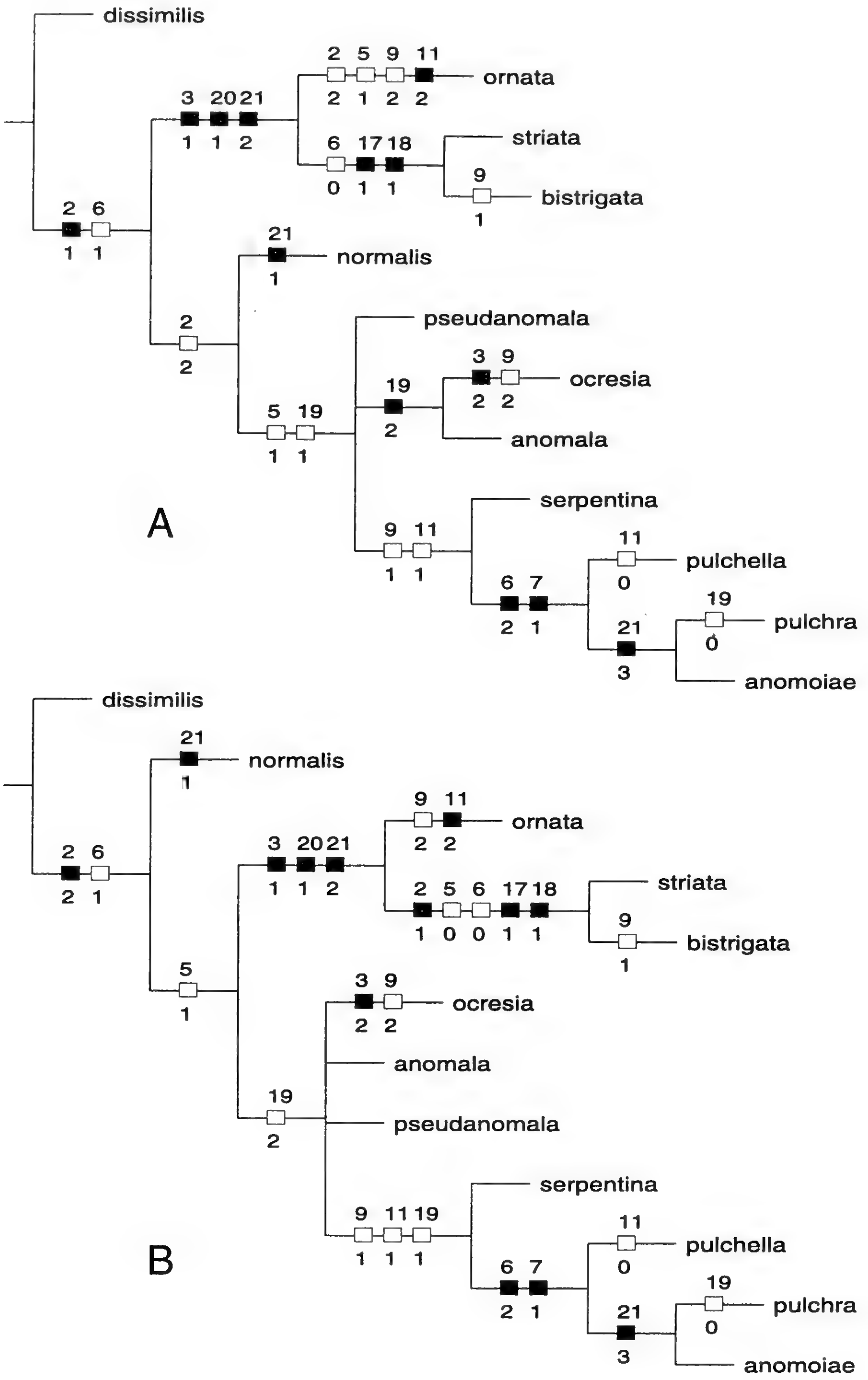

Fig. 12. Phylogenetic relationships among species of the *Anastrepha serpentina* group. Two of 95 most parsimonious trees resulting from cladistic analysis. All character state changes are shown, plotted using fast optimization.

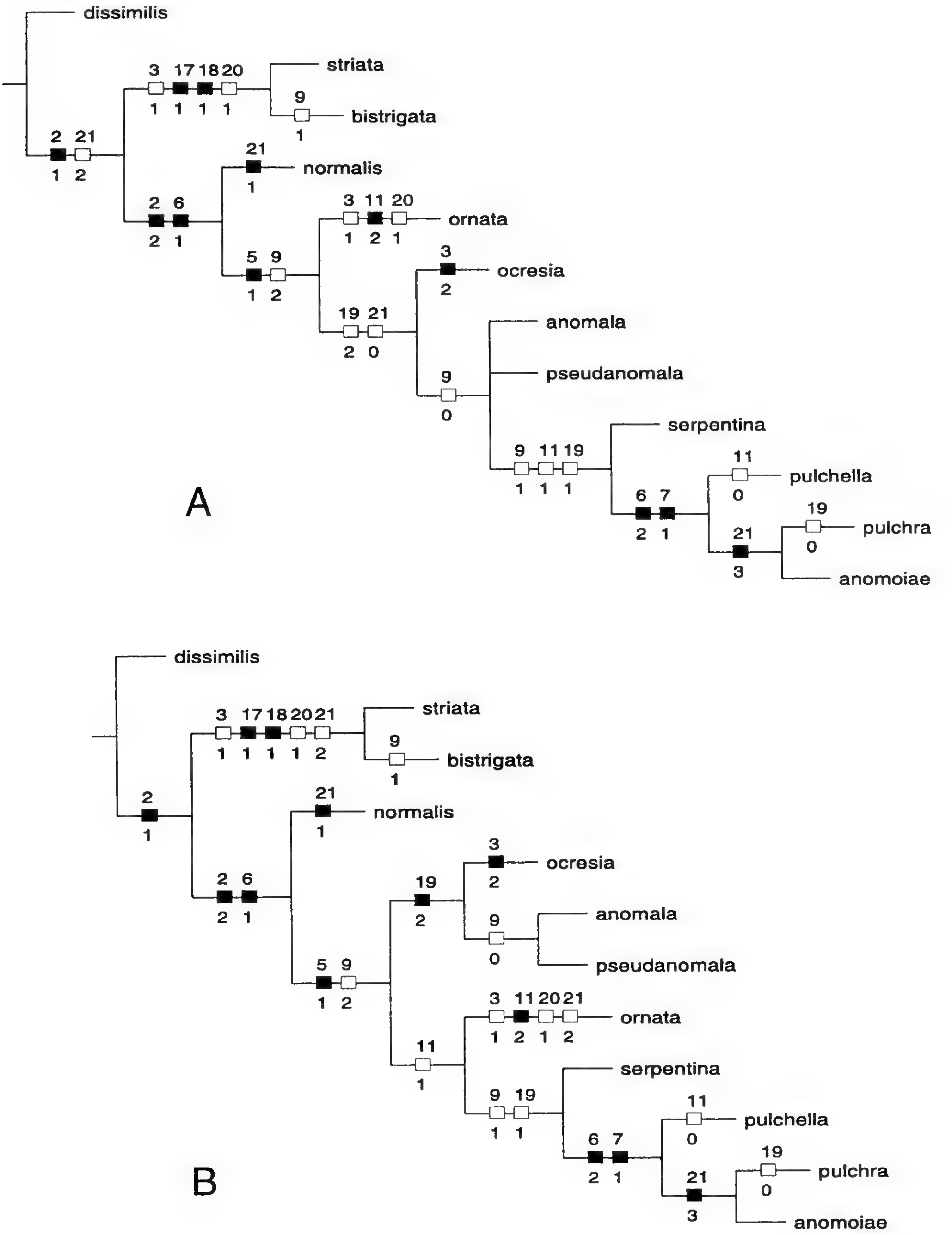

Fig. 13. Phylogenetic relationships among species of the *Anastrepha serpentina* group. Two of 95 most parsimonious trees resulting from cladistic analysis. All character state changes are shown, plotted using fast optimization.

cies known only from a male from Mexico also was excluded from the analysis.

The sister taxon of the *serpentina* group is uncertain. Norrbom et al. (1999b) proposed that the *serpentina* and *striata* groups belong to a large clade also including the *pseudoparallela, spatulata, ramosa, grandis, doryphoros,* and *fraterculus* groups. *Anastrepha dissimilis* Stone, which belongs to the *pseudoparallela* group, was chosen as the outgroup taxon as a typical representative of all of the possible sister taxa. Almost all of the species of the other groups also would be coded 0 for the characters used in the analysis, except for aculeus tip shape, which is highly variable. The matrix was analyzed using Hennig86 option ie*. Ninety-five trees of 27 steps length resulted (ci = 0.74, ri = 0.76), four of which are shown in Figs. 12 and 13, which were produced using WinClada.

The *serpentina* group, as defined here, is supported as a monophyletic group mainly by the presence of brown markings on the mesonotum and subscutellum and mediotergite (character 2), the only synapomorphy present on all 95 trees. Except in *A. ocresia,* where the brown markings are restricted to the area bordering the scuto-scutellar suture, the brown area is extensive and either somewhat U-shaped or covering most or all of the darker areas of the mesonotum. Similar extensive brown areas occur in some species of the *daciformis* group, but other characters indicate that this is due to homoplasy (Norrbom et al. 1999b). Brown mesonotal markings also occur in a few other *Anastrepha* species (e.g., *A. grandis,* some species of the *cryptostrepha* and *robusta* groups), but the different shapes of the markings and other characters also suggest that this is the result of homoplasy. The subscutellum and mediotergite are usually mostly brown in species of the *serpentina* group, although in some specimens of some species it is brown only laterally, resembling the condition in most species of the *fraterculus* species group. Because the mostly to entirely brown condition is more common in these intraspecifically variable species, I regard this as a different character state than that in the *fraterculus* group, that further supports the monophyly of the *serpentina* group. Outside of this group, it is uncommon in *Anastrepha,* occuring in some species of the *grandis, daciformis, cryptostrepha* and *robusta* groups. Only the former species group appears to be relatively closely related to the *serpentina* group (Norrbom et al. 1999b, McPheron et al. 1999).

McPheron et al. (1999) included four species of the *serpentina* group in their phylogenetic analysis of *Anastrepha* based on mitochondrial DNA sequences. They found strong support for the monophyly of *A. serpentina* + *normalis* (as "n. sp. nr. *anomala*") and also for *A. striata* + *bistrigata.* Both pairs of species were included in a large clade with species of the *fraterculus, spatulata, pseudoparallela,* and *grandis* species groups, but the relationships among these groups were poorly resolved. Studies of isozymes (Morgante et al. 1980, Matioli et al. 1992) have also shown strong similarity between *A. striata* and *bistrigata,* although *A. serpentina* was more similar to other species.

Relationships among the species within the *serpentina* group were not well resolved by the present analysis (see Figs. 12–13), although two clades were consistent in all 95 trees: *A. striata* + *bistrigata*; and *A. serpentina* + (*pulchella* + (*pulchra* + *anomoiae*)). The close relationship of *A. striata* + *bistrigata* is strongly supported by the shape of the posterior margin of the epandrium and the ridge on the lateral surstylus (character states 17.1 and 18.1, respectively), which are unique to these two species. The clade of *A. pulchella* + (*pulchra* + *anomoiae*) is also strongly supported, by the very broad connection of the C-band and S-band (character state 6.2), and the reduced or absent yellow area of the C-band posterior to the pterostigma (character state 7.1). The relationship of *A. serpentina* to the latter clade is supported by one or more of the following character states: distal section of S-band slender (9.1); hyaline marginal spot in cell r_1 elongated distally along costa (11.1; this can also be interpreted as arising independently in *A. serpentina* and in *A. pulchra* + *anomoiae*), and the lateral surstylus with a small basolateral lobe (19.1). None of these states is consistently hypothesized as a synapomorphy for these four species on every tree, however; character state 9.1 is usually a synapomorphy, but on some trees it may be interpreted as a synapomorphy for these species plus *A. ocresia* or *ornata,* with subsequent change to state 2 in the latter species.

The positions of the other species in the cladograms are highly variable. *Anastrepha normalis* is always relatively basal in the most parsimonious trees, arising as the sister group to a clade including all other species of the *serpentina* group (Fig. 12B; supported only if relatively darker wing pattern color (character state 5.1) is interpreted as a synapomorphy for the other species, with reversal in *A. striata* + *bistrigata*), as the sister group of a clade containing all of the other species except *A. striata* and *bistrigata* (Figs. 13A–B), as the sister group of a clade with all species except *A. ornata* + (*striata* + *bistrigata*) (Fig. 12A), or as the sister group of the clade *A. ornata* + (*striata* + *bistrigata*) (supported only if character 21.1 is interpreted as a synapomorphy, with subsequent change to state 21.2 in the other three species).

Anastrepha ocresia and *anomala* are usually somehow included in a clade also including the *serpentina* clade, *A. pseudanomala,* and/or *A. ornata,* and they are not closely grouped with *A. striata* + *bistrigata* on any of the trees. *Anastrepha pseudanomala* is highly variable in position, in part because characters 17–20 are unknown for it. It is usually within a clade including *A. ocresia, anomala,* the *serpentina* clade, and sometimes *A. ornata.* On some trees it is hypothesized as the sister group of *A. ornata* + (*striata* + *bistrigata*), but this is supported only if *A. pseudanomala* is assumed to have a subapical lateral lobe on the lateral surstylus (character state 20.1).

The relationship of *A. ornata* among the other species of the *serpentina* group is also unresolved by the present analysis. It is highly variable in position on the 95 cladograms. In some trees it is the sister group of *A. striata* + *bistrigata* (Fig. 12), a hypothesis supported by scutal microtrichial pattern (character state 3.1), lateral surstylus shape (20.1) and aculeus tip shape (21.2). In other trees (e.g., Fig. 13) it is placed variably within clades including *A. ocresia, anomala, pseudanomala,* or the *serpentina* clade. The hypothesis that *A. ornata* is more closely related to the species exclusive of *A. striata* and *bistrigata* is supported by the more extensively brown bodies of these species (character state 2.2), their broad C-band, which extends into the distal half of cell br (6.1), and the relatively dark wing pattern of all of the latter species except *A. normalis* (character state 5.1).

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CONSTRUCTION OF A DEFENSIVE TRASH PACKET FROM SYCAMORE LEAF TRICHOMES BY A CHRYSOPID LARVA (NEUROPTERA: CHRYSOPIDAE)

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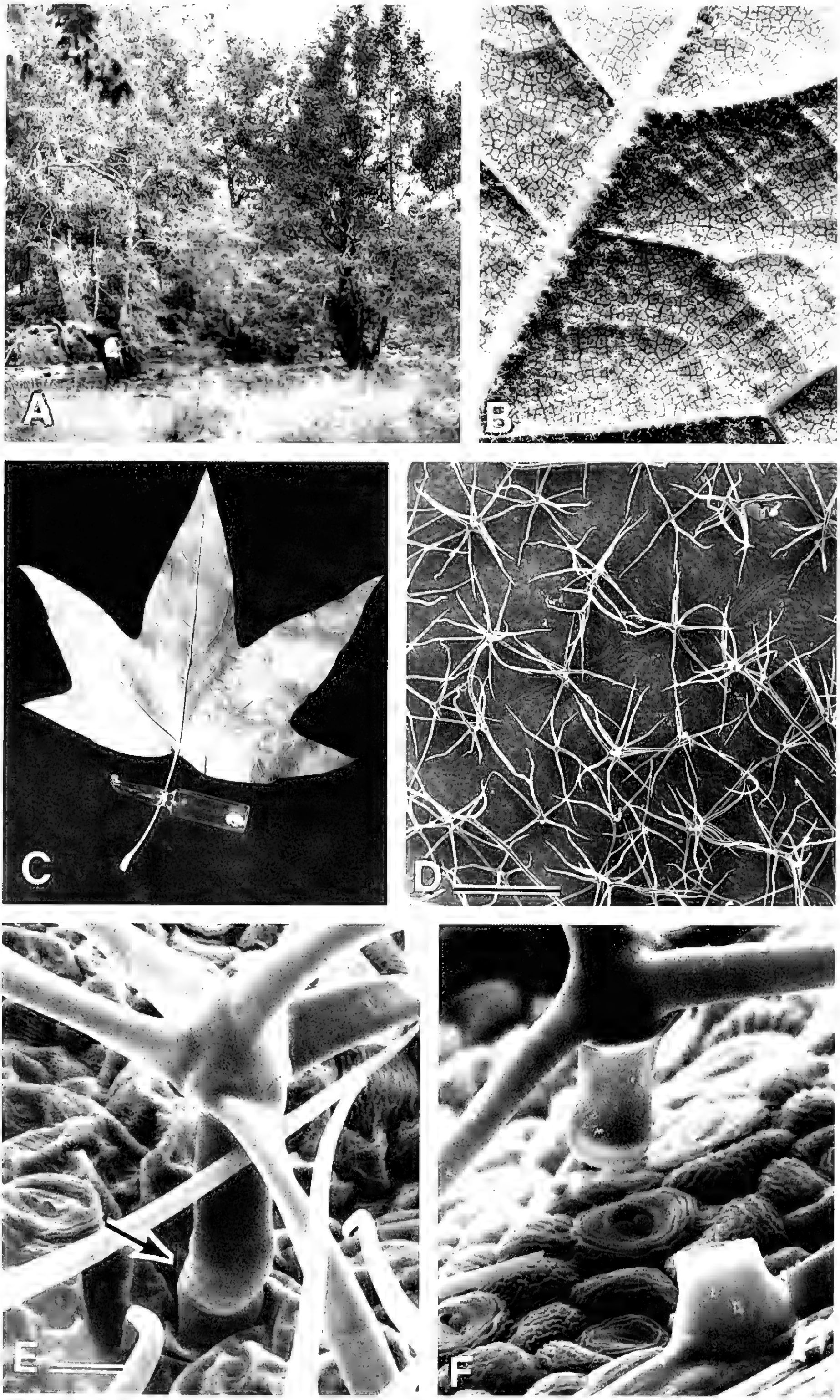
Abstract.—The behavior of a chrysopid larva from Arizona is described, identified as *Ceraeochrysa lineaticornis* (Fitch), which constructs its trash packet from the trichomes of sycamore leaves (*Platanus wrightii* S. Watson). The trichomes are particularly dense on the underside of the leaves. To fashion the packet, the larva uses trichomes stuck loosely to the leaf, and others that it plucks from the leaf surface. The packet on the mature larva weighs on average 2.2 mg, an equivalent of approximately two leaf undersides worth of trichomes. Evidence is presented indicating that the packet provides the larva with protection against predation. It is argued that the trichomes are defensive in the sycamore tree itself, and that the chrysopid provides yet another example of an insect that benefits from utilization of a plant defense. Interestingly, the chrysopid benefits the sycamore tree itself. Although it usurps the tree's defense, it aids the tree by preying on a specialist herbivore, the tingid, *Corythucha confraterna* Gibson, which feeds on the sycamore tree unbothered by the trichomes.

Key Words: animal defense, Neuroptera, Chrysopidae, *Ceraeochrysa lineaticornis,* plant defense, trichome, insect-plant interaction

Many chrysopid larvae have the habit of collecting exogenous materials and placing them on their backs, forming so-called trash packets that they retain throughout larval life (Smith 1922, Canard et al. 1984). The materials they use to fashion the packets are variable and may consist of vegetable matter, arthropod remains, insect waxes, or general debris (Smith 1922, Slocum and Lawrey 1976, New 1969, Eisner et al. 1978, Canard et al. 1984). Existing evidence indicates the packets act as physical shields that provide the larvae with protection against insectan predators (New 1969, Principi 1946, Eisner et al. 1978). Not all chrysopid larvae are trash carriers, but those that are, are obligatorily so, and the priority that larvae give to forming trash packets has a significant genetic component (Milbrath et al. 1993, Tauber et al. 1995).

Here we describe the behavior of a chrysopid larva that constructs its packet from trichomes that it takes from the leaves of sycamore trees (*Platanus wrightii* S. Watson) in Arizona. We present data on the feeding habits of the larva, as well as on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how the packet is constructed and used in defense. Our observations were made in the hamlet of Portal, Cochise County, Arizona, in 1967 (September) and 1982 (August). We refrained from publishing earlier because we had failed to obtain a definitive identification of the chrysopid. This problem has now been remedied, thanks to the courtesy of Catherine and Maurice Tauber, who have informed us that the chrysopid is *Ceraeochrysa lineaticornis* (Fitch) (voucher specimens have been deposited in the Cornell University Insect Collection).

MATERIALS AND METHODS

Field site.—We first noted the larvae on a group of sycamore trees growing on the banks of Cave Creek, in Portal itself, on the grounds of the Cave Creek Ranch, where we were in residence (Fig. 1A). We subsequently found them also on sycamore trees near Cave Creek, up to several miles upstream from the original location. The larvae were readily spotted by their white trash packet, which rendered them extremely conspicuous against the green color of the sycamore leaves on which they were found (Fig. 2A). As they scurried about, they resembled tiny ambulatory cotton wads. Careful scrutiny of the visually accessible lower branches of the trees usually revealed presence of many larvae per tree.

Maintenance of larvae.—Larvae were maintained on freshly clipped sycamore leaves in plastic containers of various sizes, including Petri dishes. In the field, larvae had been found on repeated occasions feeding on a tingid, *Corythucha confraterna* Gibson, whose colonies were of common occurrence on the sycamore leaves. Captive chrysopids were therefore always provided with some leaves that were tingid-infested. They took readily to the tingids, and appeared to feed on the nymphs only. Maintained on this diet many of the larvae went on to pupate and develop into adults. As is typical for trash-carrying chrysopids, larvae retained the trash packet as an outer covering of their cocoon when they pupated. The cocoons therefore have the same appearance as the larvae, except that they are non-ambulatory. In the field we found several cocoons on the trunks of sycamore trees. Most larvae that we used in our experiments were probably in their last instar.

Electronmicroscopy.—For examination with the scanning electronmicroscope, specimens (chrysopid larvae, pieces of sycamore leaf) were preserved in the field in 70% ethanol, then critical point dried and gold coated in the laboratory.

Predation tests.—Of the predators used, the reduviid, identified as *Pselliopus latispina* Hussey, is doubtless a natural enemy of the chrysopid. It occurred commonly on the leaves and branches of the sycamore trees themselves, and was once actually observed feeding on a *C. lineaticornis* in the field.

The ant used in predation tests, *Pogonomyrmex barbatus* (Smith), may not itself be a primary enemy of the chrysopid, but there can be little question that ants as such figure among the larva's natural predators. We routinely observed ants foraging singly on the leaves, branches and trunks of the sycamore trees.

Statistics.—Numerical averages are given as mean ± S.E.

RESULTS

The trichomes.—Both surfaces of the sycamore leaves bear trichomes, but the structures are much more densely distrib-

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Fig. 1. A, Stand of sycamore trees on which the chrysopid larva was discovered (Portal, AZ). B, Close-up of underside of sycamore leaf showing trichomes. C, Underside of sycamore leaf from which the trichomes have been removed; the detached trichomes form the wad seen in the ampule. D, Enlarged view of leaf underside (scanning electronmicrograph). E, Base of a trichome showing the hinge (arrow). F, Base of a trichome that has been torn off at the level of the hinge. Reference bars: D = 0.5 mm; E = 20 μm.

uted on the underside (Figs. 1B, D). Individually the trichomes are usually multiply branched, and they are flexibly hinged near their base, where there is a break in the core of the shaft and the wall is reduced to a thin-walled tube (Figs. 1E, F). If one pulls on individual trichomes with forceps, they tend to detach at the level of these hinges. They evidently detach spontaneously in large numbers from the leaf surface, as evidenced by the fact that the underside of sycamore leaves usually has a loose coating of detached trichomes. Microscopic examination verified clearly that these lose trichomes had broken off at the level of the hinges.

Packet construction.—Removal of the trash packets from the larvae could be effected easily by teasing away the trichomes with forceps. Eight larvae that were thus denuded and re-released into their leaf-containing enclosures, commenced reloading almost at once. In typical chrysopid fashion (New 1969, Principi 1940, Smith 1922), using their jaws as a two-pronged fork, they scooped up load upon load of trichomes and placed these upon their backs (Figs. 2C–F). Most often they procured trichomes from the clusters of available loose ones, but they also pried many off with their jaws. It seemed clear, moreover, that they were programmed to utilize sycamore trichomes only. If released in a Petri dish with general particulate debris they tended to ignore such matter, but if then offered a sycamore leaf, they usually returned promptly to the task of reloading. Like trash-carrying chrysopids generally (Canard et al. 1984), the larvae are equipped with a set of special hooked bristles that seem to serve specifically for retention of the packet. The bristles project upward in rows from the back, and there are others that project outward in clusters from a series of lateral protuberances (Figs. 4A–C).

Packet construction appeared to proceed in accord to a fixed protocol. The first pluckings were always applied to the posterior third of the body. To gain access to the site, the larvae arched that region upward and forward every time that the head flexed backward to deliver a load. Later pluckings, delivered to the more accessible anterior regions of the back, were applied without simultaneous postural adjustments of the body.

A visual demonstration of the sequence of trichome delivery during packet construction was obtained by giving denuded larvae access to trichomes of different colors. Packets were removed from a series of larvae and were then stained either in red (with acid fuchsin), in black (with chlorazol black), or kept unstained. Denuded larvae that were then given access to teased apart samples of these packets, in the sequence of black (for 30 min), to unstained (for 20 min), and to red (for 60 min), constructed packets in which the trichomes were laid out in three colored bands, in the sequence red, white, and black from fore to aft (Fig. 2B).

Package repair.—Use of stained trichomes also yielded visual evidence of the precision with which the larvae are able to repair damage to their package. Four larvae, bearing natural unstained packets, were treated as follows:

(1) Trichomes removed from center of packet, leaving the larva with a ring-shaped shield.

(2) Posterior half of packet removed.

(3) Left half of packet removed.

(4) No trichomes removed (control).

The larvae were then confined with a supply of black trichomes, and checked for condition of their packets after 24 hours. The results were as follows:

(1) Center of ring filled with unstained trichomes. Periphery of packet loosely laden with black trichomes. Larva had evidently repaired the hole in the packet with trichomes from the periphery of the packet. New trichomes had been added to the periphery to replace those used in the repair of the hole.

(2) Posterior half of packet repaired, but

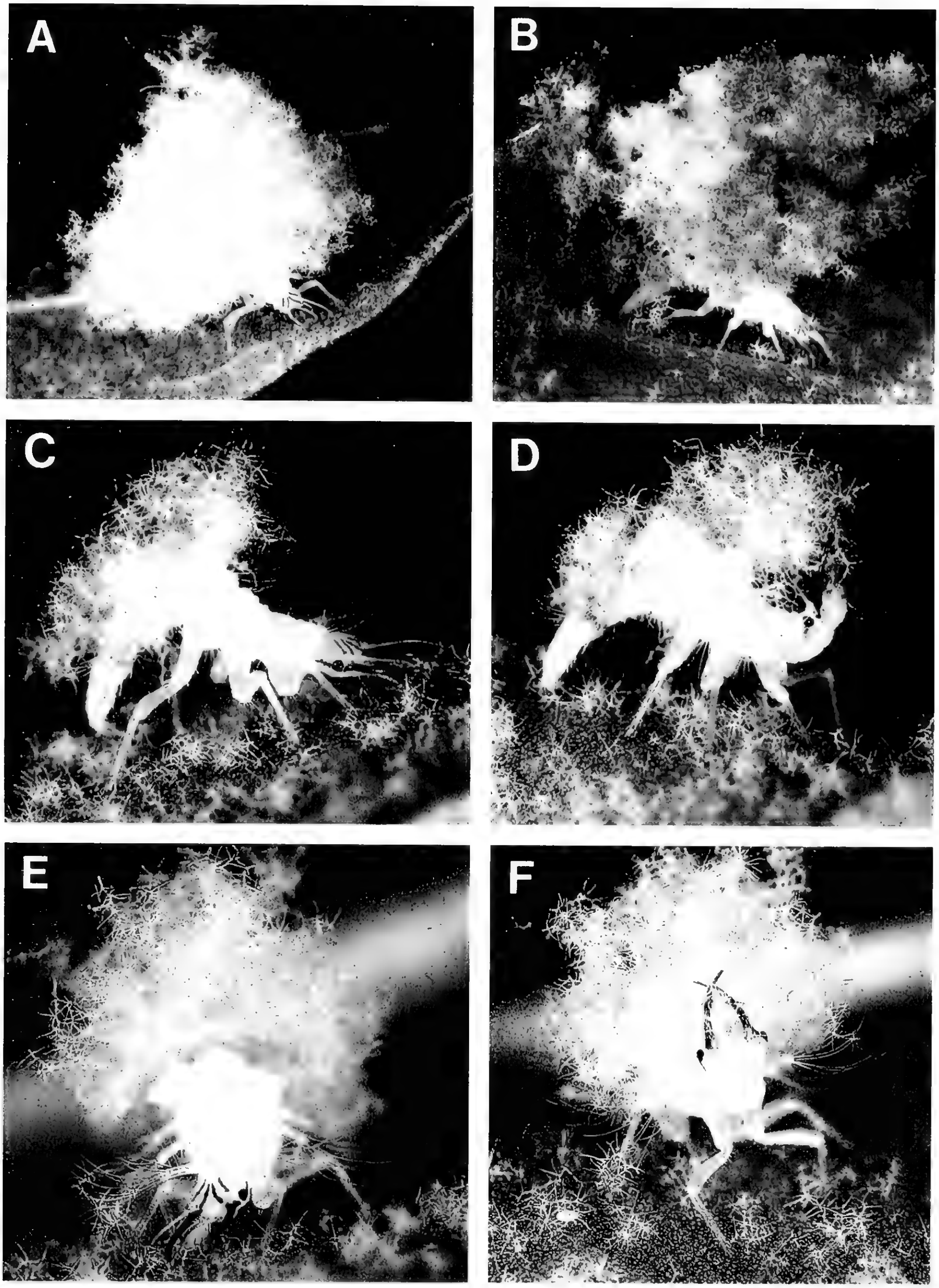

Fig. 2. A, Full-grown larva. B, Larva that has formed a packet from pre-stained trichomes (see text). C, D, Larva, in lateral view, in the process of building its packet. In C it is scooping up trichomes with the mouthparts; in D it is adding the trichomes to the packet. E, F, Same as preceding pair, but in frontal view.

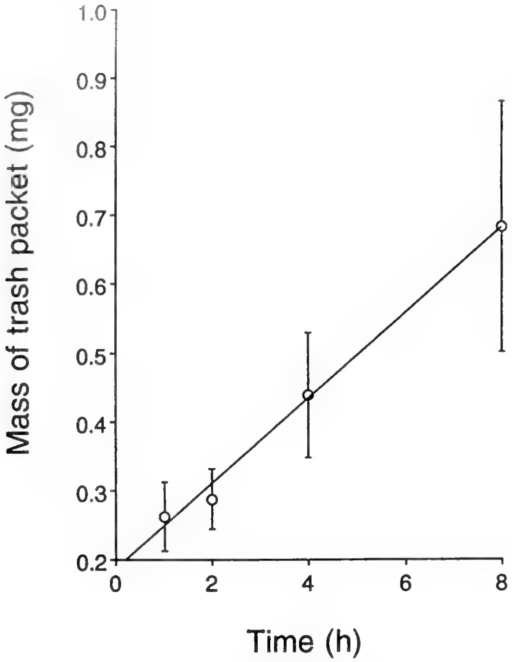

Fig. 3. Regeneration of packet by denuded larvae, expressed as mass of packet formed over time. Best fit equation is shown ($y = 0.185 + 0.062$; $R^2 = 0.994$, $P < 0.001$).

with unstained trichomes. Front half of packet made up mostly of black trichomes. The larva evidently repaired the rear of packet with trichomes from the front, and replaced the trichomes removed from the front with ones newly acquired.

(3) The missing left half of packet was restored with newly acquired black trichomes. Only few new trichomes had been added to the right half of the packet.

(4) The entire packet had been augmented by a sparse uniform addition of new black trichomes.

It is clear from these results that the larvae are able to repair their packet, and that in so doing they do not merely fill in damaged sites with newly acquired trichomes. They are able to effect repair by repositioning existing trichomes, and they correct for any resulting inequities in trichome distribution by bringing into place newly scooped up trichomes. Thus, the larvae have not only a sense of what is missing in a damaged packet but an elaborate mechanism for repairing the damage. Particularly remarkable is the larva's ability to move trichomes from one area of the packet to another. Casual observation reveals that they effect such relocation both by use of the jaws and by a sort of wave-like peristaltic action of the abdomen, whereby trichomes are transferred from one set of bristles to the next. Such peristaltic action was also noted at times during the package rebuilding undertaken by denuded larvae.

Trichome load of sycamore leaves.—Two procedures were adopted for determining the mass of trichomes per unit surface area of sycamore leaf underside.

One procedure involved taking a sycamore leaf, determining its surface area (by weighing a piece of paper in the shape of that leaf, and referencing this weight to that of a piece of known area of the paper), then removing the trichomes from the leaf underside (with forceps and by scraping with a scalpel) and weighing the trichomes (Fig. 1C). Removal of trichomes was judged to be 90% complete. The leaf (90.3 cm^2 surface area) yielded 1.2 mg trichomes, an equivalent of 13.3 μg per cm^2 of leaf underside.

The second procedure involved using denuded larvae to effect the trichome removal from a leaf. The leaf was exposed (underside up, with the upper side inaccessible) to two sets of 3 larvae each, operating in sequence for a combined period of 3 hours, by the end of which time the leaf underside was estimated to have lost 90% of its trichomes. The combined mass of the trash packets (which none of the larvae had completed in the time allocated) was 1.0 mg. It follows from this value, and from the area of the leaf (74.2 cm^2) that the leaf had yielded 13.5 μg trichomes per cm^2 of underside.

Packet construction.—To obtain some measure of the rate at which the larvae construct their packets, 32 larvae were denuded and their packets weighed. They were then individually confined in plastic enclosures

Table 1. Packet regeneration of denuded larvae. See also Fig. 3. N = 8 per category, except for 8-hour category, where N = 6.

Time since larvae were denuded (hours)	New packet	
	Mass (mg)	Proportion of original packet
1	0.263 ± 0.050	0.149 ± 0.047
2	0.288 ± 0.044	0.143 ± 0.021
4	0.438 ± 0.091	0.221 ± 0.052
8	0.683 ± 0.182	0.430 ± 0.167

containing fresh sycamore leaves, and allowed to reload for 1, 2, 4, or 8 hours. Eight larvae were initially assigned to each time category, but the sample size of the 8-hour group was reduced to 6 because 2 of the larvae had affixed themselves, preparatory to pupation, during the experimental period. At the end of the assigned times, the larvae were again denuded and their packets weighed.

From the data it was possible to calculate, first of all, the average mass of the initial trash packets of the larvae (in other words, the average mass of packets of nearly full grown field-collected larvae). That mass was 2.16 ± 0.13 mg (range = 0.70–3.30 mg). In addition, a value could be obtained for each larva of the fraction of the initial packet that had been rebuilt in the time period assigned to that larva. The mean of such values, for each of the four larval categories, is given in Table 1, which also presents averages for the net mass of packet material gathered in the times allocated. A graphic representation of the latter values (Fig. 3), shows packet reconstruction to proceed at a steady rate, at least during the initial 8 hours of rebuilding.

Predation tests: reduviid.—Five nymphs of *P. latispina* were set up in plastic containers and individually offered equal numbers (one of each, or four of each) of packet-bearing and denuded larvae. The test chambers were checked visually at intervals, and survivorship of the larvae was recorded after 12–24 hr. Of the 12 denuded larvae that were offered, only three survived. By contrast, of the 12 shield-bearers, nine survived. Some of the packet-bearing larvae were used with more than one of the reduviids. Inspection of the cages during the experimental period had revealed some of the details of the encounters. Denuded larvae tended to be grasped the moment they were located, then promptly impaled on the reduviid's proboscis and sucked out (Fig. 4G). Packet-bearing larvae, in contrast, were held by the bug with the forelegs, repeatedly probed with the proboscis (Fig. 4F), but then often released. We suspect that release was a consequence of the reduviid's proboscis being too short to reach through the packet to the body of the larva. This interpretation is supported by an early observation in which a few larvae that were partly denuded and offered to *P. latispina,* were eaten.

Predation tests: ants.—The tests were set up on barren ground, about 0.5 m from the nest entrance of a *P. barbatus* colony. Tapping the ground above the nest had thrown the ants into a state of agitation and they had emerged from the nest in numbers to mount guard around the entrance. Six of 8 denuded larvae released on the ground were encountered by individual ants and carried off. They were small relative to the ants and were not always noticed by the ants when first released. In fact, it was only upon the second or third presentation that the six larvae were taken. Of 8 packet-bearing larvae that were similarly released, only one was taken, even though they were all also retested individually two or three times. The larvae were encountered repeatedly by individual ants, but they "froze" when contacted, and the ants, which in their palpations appeared to touch the packet only (Fig. 4E), were quick to abandon the assault.

DISCUSSION

While our predation data are scant, and our predation tests not nearly as satisfactory in design as we would have liked, it seems reasonable to conclude that the trichome

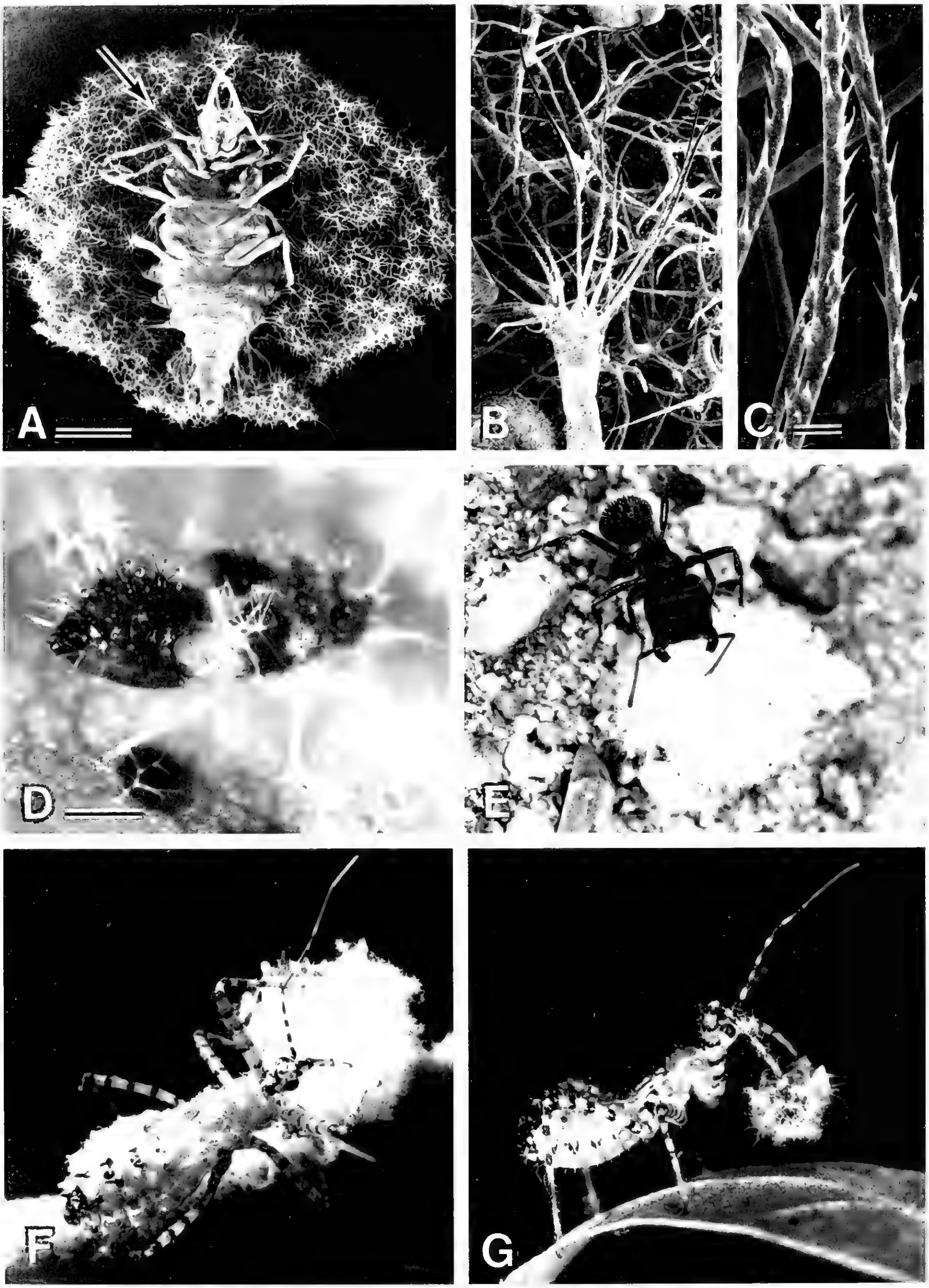

Fig. 4. A, Fully loaded larva in ventral view (scanning electronmicrograph); arrow points to one of the setose lateral protuberances that serves for retention of the packet. B, Enlarged view of a lateral protuberance. C, Detail of setae from a lateral protuberance; the barbs presumably help retain the packet. D, Nymph of the tingid *Corythucha confraterna*; note glistening droplets of secretion at tip of glandular hairs. E, An ant (*Pogonomyrmex barbatus*) inspecting a chrysopid larva. F, Reduviid nymph (*Pselliopus latispina*) probing a packet of a chrysopid larva. Most such inspections resulted in the larva being released. G, Reduviid feeding on a denuded larva. Reference bars: A = 1 mm; C = 20 μm; D = 0.5 mm.

packet of the *C. lineaticornis* larvae is a protective structure. While ours may be the first demonstration that the trash packet of a larval chrysopid can shield against the attack of a reduviid, work with other chrysopid larvae had shown the packets to provide effective defense against other Hemiptera (New 1969) and ants (Principi 1946, Eisner et al. 1978). The strategy of carrying overhead shields among insects is, of course, not restricted to chrysopid larvae. Classic examples are provided by chrysomelid beetle larvae, including notably tortoise beetle larvae (Olmstead and Denno 1992, 1993; Gómez et al. 1999; Müller and Hilker 1999; Eisner and Eisner 2000), in which the shields are usually fabricated in part with feces. By virtue of the fecal component, such shields have the capacity to deter by chemical in addition to physical action (Gómez et al. 1999), a property that sets them apart from chrysopid packets. To our knowledge, chemical noxiousness has never been demonstrated for a chrysopid packet.

It was of some interest to find that the *C. lineaticornis* larva fed on a tingid, and specifically on the nymphs thereof. Tingid nymphs, including those of *C. confraterna* (Fig. 4D), are endowed with glandular hairs (Livingston 1978), which in some species have been shown to produce a mixture of aromatic and alicyclic acetogenins (Oliver et al. 1990), potentially deterrent to predators. *Ceraeochrysa lineaticornis* is evidently undeterred by this glandular material.

Packet construction is clearly a matter of high priority for the larva. When denuded it always made prompt efforts to rebuild the packet, and when packets were partially destroyed it always proceeded to repair the structure. Packet construction has been shown to be a matter of priority also in another chrysopid, *Chrysopa slossonae* (Banks) (Eisner et al. 1978, Milbrath et al. 1993), and given that trash packets are doubtless defensive in chrysopids generally, they are probably maintained fastidiously by all larvae that possess them. In *Ceraeochrysa cincta* (Schneider), for instance, a species in which the larva cloaks itself with the wax of homopteran prey, the larvae engage in packet construction immediately upon descending from the egg along the egg stalk (Mason et al. 1991).

Packet construction from sycamore trichomes is a slow process. After a period of 8 hours, nearly full grown larvae that bore packets weighing on average about 2.2 mg before being denuded, had reconstituted an equivalent of only about 40% of the original shield. It can be inferred from this that the rebuilding of an entire shield should take such larvae over a day. In fact, if one assumes reloading to proceed indefinitely at the linear rate prevailing over the first 8 hours (Fig. 3), one can calculate from the best-fit equation pertinent to that rate that it would take larvae on average nearly 32 hours to reproduce the initial packet.

The number of trichomes that go into the construction of the larval packet is substantial. A mature larva, bearing an average-sized packet of 2.2 mg, carries an amount of trichomes equivalent to what is obtainable from two sycamore leaf undersides.

Are the trichomes defensive for the sycamore itself, and does *C. lineaticornis* exemplify yet another case of utilization by an insect of defenses that evolved in the first place for protection of a plant? Sycamore trichomes can be envisioned to serve in a multiplicity of capacities. They could, for example, act to trap a layer of "dead air" directly adjacent to the leaf surface and by so doing provide for retardation of evaporative water loss from the leaves. But this does not rule out the possibility that the trichomes serve also in defense. Tightly spaced and barbed, the trichomes could well be a hindrance to many an ambulatory arthropod. The chrysopid and its tingid prey could thus be viewed as specialists that have managed to access a niche not generally open to colonization. The tingid has come to cope with the plant's defense and has become the plant's enemy. The chrysopid in contrast, is essentially the plant's ally. Although it usurps the plant's defense, and uses the weaponry for it own purpose, it feeds on the tingid, and by so doing has become the plant's "delousing" agent. Losing a fraction of its trichomes to the chrysopid must thus be viewed as being beneficial to the sycamore.

ACKNOWLEDGMENTS

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TAXONOMIC REVISION OF THE GENUS *MEGOURA* BUCKTON (HEMIPTERA: APHIDIDAE) FROM THE KOREAN PENINSULA WITH THE DESCRIPTION OF A NEW SPECIES AND A KEY TO THE WORLD SPECIES

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Abstract.—Three species of *Megoura* are recognized from the Korean Peninsula, among which ***Megoura nigra* Lee, n. sp.**, and the fundatrix, hitherto unknown morph, of *M. crassicauda* Mordvilko 1919 are described. *Megoura nigra* can be distinguished easily from other species of *Megoura* by its dark brown body color in life. It also differs from the closely related species *M. crassicauda* and *M. viciae* Buckton 1876 by its relatively long ultimate rostral segment, 0.88–1.00× 2HT (0.63–0.87× in the latter two species), mandibular laminae, antennal segment I, abdominal tergite III, and genital plate with 6–8, 13–20, 16–21, and 24–33 hairs respectively (3–5, 8–15, 12–18, and 14–23 in the latter two species). After examining and measuring the specimens of all known *Megoura* spp., a worldwide key to species is presented.

Key Words: Hemiptera, Aphididae, *Megoura,* Korea, key to world species

The Genus *Megoura* Buckton 1876 is a small genus of the tribe Macroshipini (Hemiptera: Aphididae) with six valid species described from the Palearctic Region; three (*M. crassicauda* (Mordvilko 1919), *M. lespedezae* (Essig and Kuwana 1918), and *M. brevipilosa* (Miyazaki 1971)) from East Asia, one (*M. dooarsis* (Ghosh and Raychaudhuri 1969)) from the Indian subregion, and two (*M. viciae* Buckton 1876 and *M. litoralis* Müller 1952 in Börner 1952) from Europe, Central Asia, and the Middle East (Remaudière and Remaudière 1997, Blackman and Eastop 2000, Miyazaki 1971). This genus is characterized by having swollen siphunculi and, so far as is known, living only on limited genera of Leguminosae: *Vicia* Tourn. ex Linn., *Lathyrus* Linn., *Hedysarum* Linn., *Indigofera* Linn., *Cajanus* DC., *Desmodium* Desv., and *Lespedeza* Michx. All known species are green in life, and some species have antennae, legs, siphunculi, and cauda dark brown.

In the Korean Peninsula, two species (*M. crassicauda* and *M. lespedezae*) have been recorded by Okamoto and Takahashi (1927) and Paik (1965, 1972). These two species are very common throughout the Korean Peninsula where their host plants occur.

In 1999, we collected dark brown colonies of *Megoura* on *Vicia venosa* Maxim. Subsequently, we have collected and examined many samples of *Megoua* throughout South Korea including Jeju Island. Moreover, many South Korean specimens stored in the National Institute of Agricultural Sciences and Technology, and North Korean specimens collected by Jan Havelka in 1985, 1987, and 1988, were also examined. As a result, three species are recognized, among which the dark brown *M. nigra* is described as new to science and the fundatrix, hitherto unknown morph, of *M. crassicauda* is reported for the first time. In addition, after examining and measuring the specimens of all known *Megoura* spp., a worldwide key to the species of the genus *Megoura* is presented.

Abbreviations used for descriptions in this paper are as follows: Ant.I, II, III, IV, V, VIb = antennal segment I, II, III, IV, V, and the base of Ant.VI, respectively; PT = processus terminalis; URS = ultimate rostral segment; ML = mandibular laminae; 2HT = second segment of hind tarsus; SIPH = siphunculus.

Names of host plants were checked by "The Plant Names Project (1999). International Plant Names Index. Published on the Internet; http://www.ipni.org [accessed 29 September 2001]."

All specimens examined in this paper are housed in the National Institute of Agricultural Science and Technology (NIAST), Suwon, Korea, and the Institute of Entomology, Czech Academy of Sciences (IE CAS), Ceske Budejovice, Czech Republic. The holotype and paratypes of *M. nigra*, n. sp., are housed in NIAST.

Megoura Buckton 1876

Megoura Buckton 1876: 64 (type species: *Megoura viciae* Buckton 1876).

Drepaniella del Guercio 1913: 188 (type species: *Aphis viciae* Kaltenbach 1843, not Fabricius 1781 = *Megoura viciae* Buckton 1876).

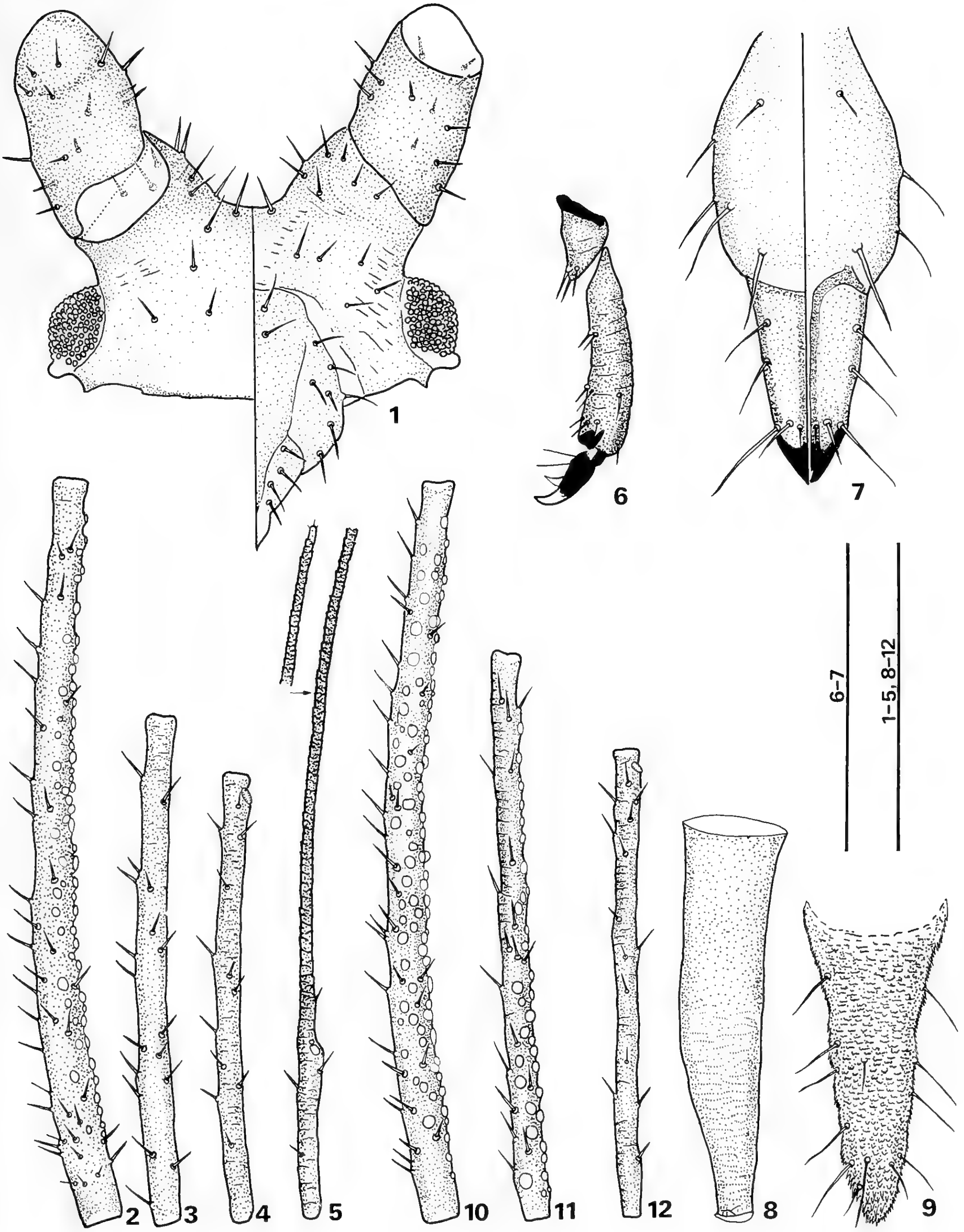
Neomegouropsis Ghosh, Basu and Raychaudhuri 1977: 584 (type species: *Megouroparsus dooarsis* Ghosh and Raychaudhuri 1969).

***Megoura nigra* Lee, new species**

(Figs. 1–12, Table 1)

Description.—*Alate viviparous female.* Color (in life): Entirely dark reddish brown, almost black. Color (in macerated specimens): Head including antennae and rostrum dark brown. Prothorax pale brown; meso- and metathorax pale with spinal and marginal pigmented sclerites. Abdomen pale with marginal and occasionally dorsal small pigmented sclerites at base of hair; ante- and postsiphuncular sclerite well pigmented; tergite VII and VIII with pale brown horizontal bands. Legs dark brown except bases of femora and tibiae from base to distal 1/5. SIPH and cauda dark brown.

Morphology: Body 3.13–4.28 mm long. *Head:* Smooth with 4 pairs of acute dorsal hairs; antennal tubercle well developed, bearing 5–7 hairs, frons with 1 pair of ventral hairs. Antenna 3.43–4.63 mm long, as long as or longer (0.99–1.29×) than body length; Ant.I smooth with 13–20 hairs; Ant.II smooth with 6–8 hairs; Ant.III smooth with 28–64 secondary rhinaria; longest hair on Ant.III 0.60–0.85× the basal width of segment; Ant.IV and Ant.V imbricated; primary rhinarium on Ant.V ciliated, longest diameter distinctly shorter than middle width of Ant.V; Ant.VIb imbricated with 3–4 hairs; PT imbricated, 3.42–4.13× as long as base of Ant.VIb. Rostrum attaining frontal margin of hind coxae; clypeus with 4 hairs; mandibular laminae (ML) with 6–8 hairs; URS wedge-shaped, as long as or slightly shorter (0.88–1.00×) than 2HT with 2 pairs of secondary hairs. *Thorax:* Prothorax with 2–3 mesial and 3 marginal hairs anteriorly. Hind coxae spinulated with ca. 14 acute hairs; hind trochanter smooth with 3 hairs; hind femur smooth, more than 2× as long as SIPH; hind tibia smooth; first tarsal chaetotaxy 3:3:3; 2HT imbricated with 2–4 dorsal, 6–7 ventral hairs. *Abdomen:* Abdominal dorsum membranous with marginal pigmented sclerites on abdominal tergites II–IV, and small pigmented sclerites at base of hairs; ante- and postsiphuncular sclerites large, well developed; 16–21 hairs on tergite III including marginal ones, 6–11 on tergite VI between SIPH, and 4–8 on tergite VIII; genital plate weakly pigmented, spinulated with 2–4 median long hairs and 22–30 short hairs on posterior margin. SIPH 1.09–1.33× cauda, swollen in middle, middle diameter 2× as wide as the distal diameter. Cauda elongated, tapering to apex with 10–



Figs. 1–12. *Megoura nigra.* 1–8, Apterous viviparous female. 1, Dorsal and ventral surface of head. 2, Antennal segment III (Ant.III). 3, Antennal segment IV (Ant.IV). 4, Antennal segment V (Ant.V). 5, Antennal segment VI (Ant.VIb + PT). 6, Tarsal segments. 7, Third and ultimate segment of rostrum (URS). 8, Siphunculus. 9, Cauda. 10–12, Alate viviparous female. 10, Antennal segment III (Ant.III). 11, Antennal segment IV (Ant.IV). 12, Antennal segment V (Ant.V). Scale bars equal 0.5 mm for Figs. 1–5, 8–12 and 0.25 mm for Figs. 6–7.

15 hairs, denticulated at basal half, spinulated in a group of 2–3 spinules at distal half.

Alate viviparous female. Color (in life): Thorax entirely dark brown. Abdomen with large marginal sclerite on each segment. Wings transparent with narrow dark pigmentation along veins and stigma. *Morphology:* Ant.III and Ant.IV with 62–89 and 19–37 secondary rhinaria respectively. Otherwise like apterous viviparous female.

Apterous oviparous female. Hind tibia swollen with numerous pseudosensoria. Otherwise like apterous viviparous female.

Alate male. About 24 and 18 secondary rhinaria on Ant.IV and Ant.V, respectively. Abdomen with additional dark horizontal pigmented sclerites on each segment. Otherwise like alate viviparous female.

Measurements: See Table 1.

Type material.—Holotype. Apterous viviparous ♀, South Korea: Gyounggi-do: Pocheon: Gwangreung National Arboretum, 11.v.2001, Slide no. 010511-sh-01(apt.5), on *Vicia venosa* Maxim.

Paratypes. 32 apterous viviparous ♀, 39 alate viviparous ♀, same collection data of holotype; 15 apterous viviparous ♀, same locality of holotype, 21.v.1999, coll. #990521-16sh, on *V. venosa*; 2 alate ♂, 3 oviparae, same locality, 19.x.2000, coll. #001018-sh-33, on *V. venosa.*

Biology and host plants.—So far, this species has been observed only on *V. venosa* in the Gwangreung National Arboretum, South Korea. It lives on young stems or undersides of young leaves. Males and oviparae occur in the middle of October, and it is monoecious holocycly on *V. venosa.*

Distribution.—South Korea.

Etymology.—The species name *nigra* is derived from the dark reddish brown to almost black body color in life, whereas all other species of *Megoura* are green in life.

Notes.—Morphologically, this species is similar to *M. crassicauda* and *M. viciae* from which it can be distinguished by its entirely dark brown body color (green in the latter species), relatively long ultimate rostral segment, 0.88–1.00× 2nd hind tarsus (0.63–0.87× in the latter species), 6–8, 13–20, 16–21, and 24–33 hairs on mandibular laminae on each side, antennal segment I, abdominal tergite III, and genital plate respectively (3–5, 8–15, 12–18, and 14–23 in *M. crassicauda* and *M. viciae*), and relatively long siphunculi, 1.08–1.33× cauda (siphunculi shorter than cauda in *M. crassicauda*) (see Table 1 and Table 2). It also can be easily separated from other species of *Megoura* by dark brown body color.

Megoura crassicauda Mordvilko 1919
(Figs. 13–21)

Megoura viciae crassicauda Mordvilko 1919: 327.

Rhopalosiphum viciae var. *japonicum* Matsumura 1918: 10. (Invalid by Hille Ris Lambers 1965.)

Nectarosiphum moriokae Shinji 1923: 308. (Syn. by Moritsu 1948.)

Megoura viciae japonica: Moritsu 1948: 84; Tao 1963: 183.

Megoura japonica: Okamoto and Takahashi 1927: 133.

Megoura viciae coreana Moritsu 1948: 84; Paik 1965: 72. (Syn. by Hille Ris Lambers 1965.)

Nectarosiphum moriokae Shinji 1923: 308. (Syn. by Moritsu 1948.)

Amphorophora lathyri Shinji 1924: 365. (Syn. by Moritsu 1948.)

Megoura lathyri: Shinji 1941: 897.

Amphorophora vicicola Shinji 1941: 773.

Megoura crassicauda: Hille Ris Lambers 1965: 195.

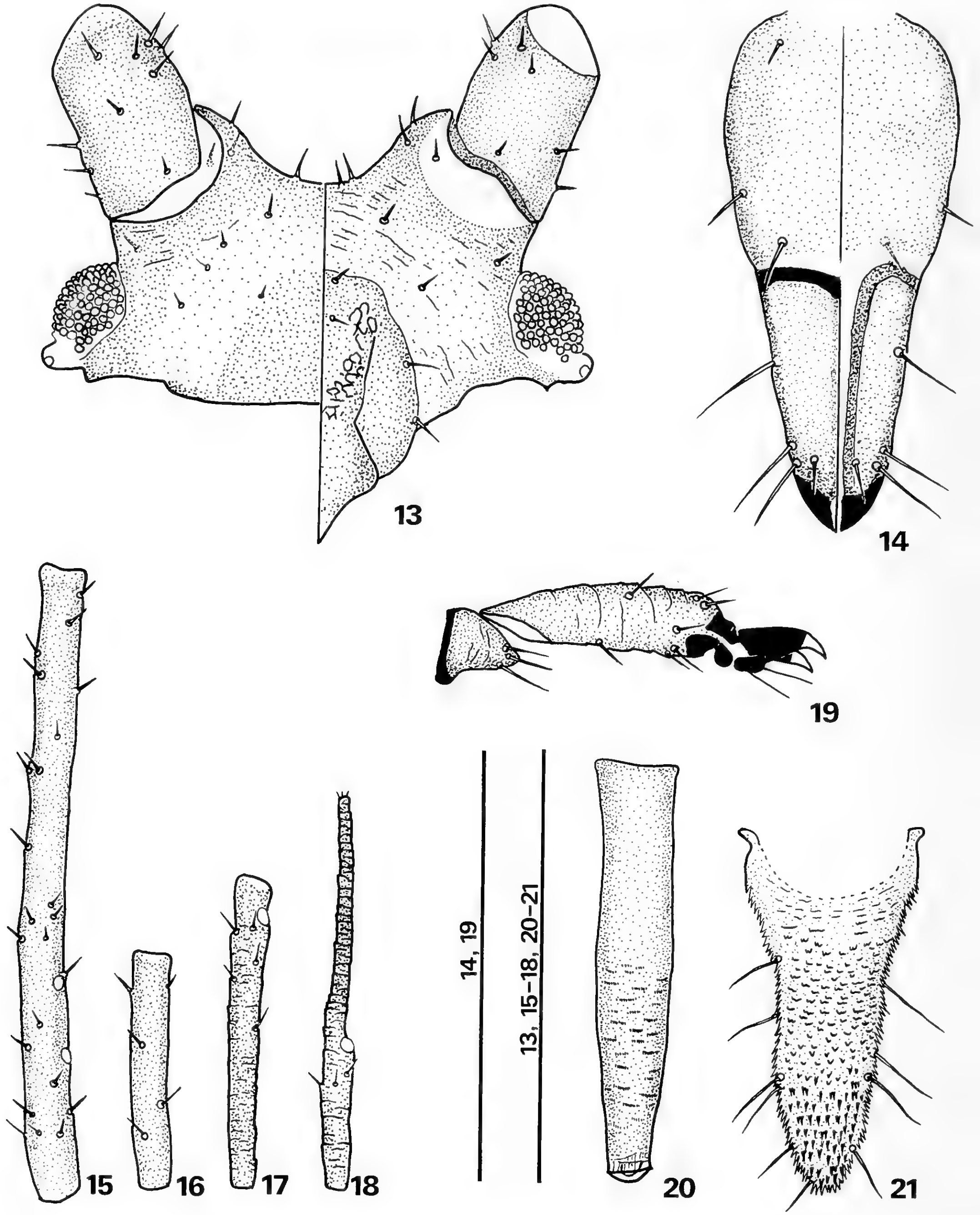
Description.—Fundatrix. Color (in life): Body green except head, antenna, legs, siphunculi, and cauda black or dark brown. Color (in macerated specimens): Head including antenna and rostrum dark brown. Thorax pale with irregular dorsal and lateral dark sclerites; legs dark brown except extreme bases of femora pale brown. Abdomen pale; antesiphuncular sclerite dark brown, postsiphuncular sclerite small; ter-

Table 1. Biometric data of *Megoura nigra.*

		Apterous vivipara (n = 10)	Alate vivipara (n = 10)
	Part	Min.–Max. (Avr.)	Min.–Max. (Avr.)
Length of (in mm)	Body from antennal tubercle to cauda	3.13–4.28 (3.75)	3.00–3.88 (3.37)
	Whole antennae	3.43–4.63 (4.13)	3.38–4.63 (4.21)
	Antennal segment III (Ant. III)	0.96–1.32 (1.17)	1.00–1.21 (1.10)
	Antennal segment IV (Ant. IV)	0.56–0.88 (0.77)	0.73–0.91 (0.82)
	Antennal segment V (Ant. V)	0.56–0.80 (0.71)	0.65–0.81 (0.73)
	The base of antennal segment VI (Ant. VIb)	0.21–0.29 (0.26)	0.23–0.29 (0.25)
	Processus terminalis (PT)	0.75–1.08 (0.98)	0.90–1.15 (1.06)
	Ultimate rostral segment (URS)	0.13–0.14 (0.139)	0.13–0.15 (0.141)
	Hind tibia	1.93–2.70 (2.39)	2.20–2.95 (0.45)
	Hind femur	1.11–1.63 (1.44)	1.19–1.63 (1.36)
	Hind tarsus II (2HT)	0.14–0.16 (0.150)	0.12–0.15 (0.14)
	Siphunculus (SIPH)	0.50–0.70 (0.60)	0.45–0.58 (0.53)
	Cauda	0.45–0.60 (0.51)	0.38–0.50 (0.45)
No. hairs on	Antennal segment I (Ant. I)	13–20 (15.75)	13–19 (15.25)
	Ultimate rostral segment (URS)	4–4 (4.00)	4–4 (4.00)
	Mandibular laminae (ML)	6–8 (6.90)	6–8 (6.60)
	Tergite III	16–21 (19.00)	20–24 (22.30)
	Tergite VI between SIPH	6–11 (7.50)	5–9 (7.10)
	Tergite VIII	4–8 (5.70)	4–6 (5.50)
	Genital plate	24–33 (28.10)	23–31 (26.00)
	Cauda	10–15 (12.20)	12–14 (12.60)
No. rhinaria on	Ant. III	28–64 (53.30)	62–89 (71.90)
	Ant. IV	0–4 (0.20)	19–37 (28.85)

gite VII and VIII with transverse dark brown bands. SIPH, cauda, and genital plate dark brown.

Morphology: Body oval or short spindle-shaped. *Head:* Smooth with 4 pairs of short hairs; antennal tubercle developed with 2–5 hairs on each side; longest hair on dorsum shorter (0.7×) than basal width of Ant.III. Antenna short, 0.56–0.70× body length; Ant.I and Ant.II smooth or slightly spinulated, bearing 6–10 and 3–6 hairs, respectively; Ant.III smooth with 1–4 secondary rhinaria on basal ½; Ant.IV short, less than 0.5× Ant.III, weakly imbricated; Ant.V imbricated, bearing small primary rhinarium, longest diameter less than 0.5× as long as middle width of Ant.V; Ant.VI strongly imbricated; PT short 1.65–2.23× base of Ant.VI; longest hair on Ant.III ⅔× basal width of segment. Rostrum attaining mesocoxae; clypeus with 4 hairs; ML with 2–4 hairs on each side; URS 0.92–1.08× and 0.71–1.00× as long as 2HT and Ant.VIb, bearing 1 pair of hairs. *Thorax:* Prothorax with 1 pair of spinal hairs and 2 pairs of marginal hairs anteriorly. Hind coxae spinulated with ca. 10 hairs; hind trochanter smooth with 2–3 hairs; hind femur spinulated, 1.50–1.89× SIPH, longest hair less than 0.5× basal width of segment; hind tibia smooth, longest hair shorter than middle width of segment; first tarsal chaetotaxy 3:3:3; 2HT imbricated, bearing 3–5 dorsal hairs and 3–4 ventral hairs. *Abdomen:* Abdominal dorsum membranous with 9–11, 4–6, and 5–7 hairs on tergite III, tergite VI between SIPH, and tergite VIII respectively; longest hair on abdomninal dorsum less than 0.5× basal width of hind femur; antesiphuncular sclerite well developed; postsiphuncular sclerite small or undeveloped; tergites VII and VIII with transverse dark



Figs. 13–21. Fundatrix of *Megoura crassicauda*. 13, Dorsal and ventral surface of head. 14, Third and ultimate segment of rostrum (URS). 15, Antennal segment III (Ant.III). 16, Antennal segment IV (Ant.IV). 17, Antennal segment V (Ant.V). 18, Antennal segment VI (Ant.VIb + PT). 19, Tarsal segments. 20, Siphunculus. 21, Cauda. Scale bars equal 0.5 mm for Figs. 13, 15–18, 20–21 and 0.25 mm for Figs. 14, 19.

bands; genital plate well-pigmented, weakly spinulated with 2–6 median hairs and 12–18 short hairs on posterior margin. SIPH 1.10–1.43× cauda, 0.62–0.78× Ant.III, and 0.53–0.67× hind femur, cylindrical, slightly swollen and widest in middle, smooth at basal half, weakly spinulated on distal half. Cauda elongated tongue-shaped, spinulated ventrally in a group of 1–4 spinules, bearing 8–13 hairs.

Measurement (mininum-maximum (average) in mm): Body, 2.87–3.43 (3.12). Antenna total, 1.80–2.13 (1.93); Ant.I, 0.15–0.17 (0.16); Ant.II, 0.11–0.12 (0.112); Ant.III, 0.61–0.73 (0.66); Ant.IV, 0.20–0.28 (0.25); Ant.V, 0.29–0.36 (0.32); Ant.VIb, 0.13–0.17 (0.154); PT, 0.25–0.33 (0.29). Hind tibia, 1.25–1.48 (1.32); hind femur 0.72–0.85 (0.77); 2HT, 0.12–0.13 (0.124). SIPH, 0.45–0.50 (0.47). Cauda, 0.34–0.41 (0.37). URS, 0.25–0.33 (0.29).

Specimens examined.—Five fundatrix, South Korea: Jeju-do: Bukjeju: Oo-do: Joil-ri, 19.iv.2000, Coll.# 00417-sh-39, on *Vicia angustifolia* L. Numerous apterous and alate viviparous ♀, oviparous ♀ and alate ♂ throughout the Korean Peninsula, on *Pisum sativum* Linn., *Vicia* spp. (*amurensis* Oettingen, *angustifolia* L., *unijuga* A. Br.), and *Lathyrus japonicus* Willd.

Biology and host plants.—This species lives on young stems or underside of leaves. It is holocyclic on *Vicia* spp. (*amurensis, angustifolia, cracca, faba, segetalis* Thuill., *unijuga*), and *Lathyrus* spp. (*davidii* Hance, *japonicus*). Also collected on *Pisum sativum* in Korea.

Distribution.—Korean Peninsula, Russia (Siberia, Primorskii), Japan, China, Taiwan.

Note.—Hille Ris Lambers (1965) considered *M. viciae* subsp. *crassicauda* Mordvilko 1919 as a separate species based on "having numerous protruding rhinaria over about ⅓–⁹⁄₁₀ of antennal segment III along one side of the segment in apterae and also the antennal segment IV covered with a number of rhinaria in alate." According to our examination and measurements for European samples of *M. viciae* and East Asian samples of *M. crassicauda* from Korea and Japan, it was found that some European samples from Slovakia have up to 26 secondary rhinaria scattered on Ant. III in apterae. Conversely, some specimens of *M. crassicauda* from Korea have only 20 secondary rhinaria, mostly located in a line as like *M. viciae.* The fundatrix of *crassicauda* described here is also closely related to that of *M. viciae* described by Heie (1995). In spite of these overlapping chracteristics and similarity, all alate samples of *M. crassicauda* from Korea and Japan could be seperated by having more than 17 secondary rhinaria on antennal segment IV, whereas European *M. viciae* have no secondary rhinaria or rarely 1–7 on basal ½ of Ant.IV (see Table 2).

Megoura lespedezae
(Essig and Kuwana 1918)

Rhopalosiphum lespedezae Essig and Kuwana 1918: 57.

Myzus lespedezae: Shinji 1927: 59.

Amphorophora lespedezae: Shinji 1941: 744; Tao 1963: 184; Paik 1965: 73.

Megoura abnormis Ghosh 1970: 7. (Syn. by Ghosh 1973.)

Megoura cajanae Ghosh, Ghosh and Raychaudhuri 1971: 385.

Megoura lespedezae: Miyazaki, 1971: 49; Remaudière and Remaudière 1997: 118.

Specimens examined.—Numerous apterous viviparous ♀, alate viviparous ♀, and oviparous ♀ throughout the Korean Peninsula on *Lespedeza bicolor* Turcz.

Biology and host plants.—This species is holocycly on *Lespedeza* spp. (*bicolor* Turcz., *cyrtobotrya* Miq.). It lives on the young stem or underside of leaves.

Distribution.—Korean Peninsula, Japan, China, Taiwan, India, Switzerland (recently discovered by Giacalone and Lampel 1996).

Table 2. Morphological comparison of *Megoura viciae, M. crassicauda,* and *M. nigra.*

Morph	Characters		*M. viciae**	*M. crassicauda**	*M. nigra*
Apterous female	Body colour (in life)		Green	Green	Dark brown
	Hairs on	Ant. I	8–15 (10.9)	9–13 (10.5)	13–20 (15.8)
		ML	3–4 (3.6)	4–5 (4.3)	6–8 (6.90)
		Tergite III	12–16 (14.4)	15–18 (16.8)	16–21 (19.0)
		Genital plate	14–22 (17.7)	14–23 (18.8)	24–33 (28.10)
	Ratio	URS/2HT	0.632–0.824 (0.723)	0.684–0.875 (0.767)	0.875–1.000 (0.927)
		SIPH/cauda	0.812–1.000 (0.906)	0.963–1.185 (1.037)	1.087–1.333 (1.184)
	Secondary rhinaria on Ant. III		5–26 (14.8)	20–42 (34.3)	28–64 (53.3)
Alate female	Secondary rhinaria on	Ant. III	23–48 (33.8)	46–64 (54.9)	62–89 (71.9)
		Ant. IV	0–7 (2.0)	17–31 (24.1)	19–37 (28.85)

* Specimens measured for *M. viciae* and *M. crassicauda* in comparison with *M. nigra* sp. nov.

Megoura viciae: 2 apt. 2 al., Czech Republic: Bohemia: Karlstejn, on *Vicia faba,* No. 4531; 2 apt., 1 al., Slovakia: Viricky, 27.vi.1966, No. 10495b, on *Lathyrus nigricans*; 2 apt., 2 al., Czech Republic: Bohemia: Mt. Stozec, 25.vii.1991, No 22354, on *Lathyrus pratensis*; 2 apt., Rumania: Paniceni, 6.vii.1976, No. 15990B, on *L. pratensis*; 2 apt., 3 al., Russia: Moskva: Abramcevo, 14.vii.1967, No. 11169B, on *V. faba.*

Megoura crassicauda: 4 apt., 1 al., Japan: Chiba: Naganuma, 18.vi.1981; 2 apt., 1 al., North Korea: Pyongsong: Mt. Ryoungak-san, 15.vi.1987, No. 87HA1869, on *Vicia japonica*; 2 apt., 1 al., North Korea: Pyongyang: Bot. Garden, 2.vi.1988, No. 88HA2772, on *V. faba*; 1 apt., 1 al., North Korea: Mt. Myohang-san: Toggol, 16.vi.1985, No. 85HA796, on *V. japonica*; 1 al., North Korea: Haeju: Mt. Suyan-san, No. 87HA1587, on *V. japonica*; 5 apt., South Korea: Jeju-do: Namjeju: Daejeong: Hamo-ri, 15.viii.1998, on *L. japonicus*; 5 apt., South Korea: Ulreung Island: Naribunji, 8.vi.2000, No. 00065-sh92, on *Vicia* sp.; 5 apt., South Korea: Gangwon-do: Inje: Guidun-ri, 4.vi.1999, No. 990602-69sh. on *Vicia* sp.

KEY TO WORLD SPECIES OF *MEGOURA*

Apterous Viviparous Females

1. Cauda dark brown or black. On *Vicia* spp. or *Lathyrus* spp. 2

– Cauda pale yellow, at most fuscous. Not on *Vicia* spp. 4

2. Body totally dark brown or black in life. Tibia pale yellow except apical ⅕ in macerated specimens. Ultimate rostral segment (URS) as long as or slightly shorter (0.88–1.00×) than 2nd hind tarsus (2HT). Antennal segment I (Ant.I), mandibular laminae (ML), abdominal tergite III, and genital plate with 13–20, 6–8, 16–21, and 24–33 hairs respectively. Ant.III with usually more than 50(28–64) secondary rhinaria. On *Vicia venosa* Maxim. South Korea . . . . *M. nigra* Lee, n. sp.

– Body green except antenna, legs, siphunculus, and cauda black in life. Tibia black or dark brown in macerated specimens. URS distinctly shorter (0.63–0.87×) than 2HT. Ant.I, mandibular laminae, abdominal tergite III and genital plate with fewer hairs, 8–15, 4–5, 15–18, and 14–23 respectively. Ant.III with usually less than 40 (5–42) secondary rhinaria 3

3. Antenna with more than 20 secondary rhinaria on Ant.III scattered irregularly over ⅔ or throughout the segment. SIPH as long as or frequently longer than cauda. On *Vicia* spp. (*amurensis* Oettingen, *angustifolia* L., *cracca* Linn, *faba* Linn., *segetalis* Thuill., *unijuga* A. Br.), *Lathyrus* spp. (*davidii* Hance, *japonicus* Willd), and *Pisum sativum* Linn. East Asia (Korea, China, Taiwan, Japan, Russia (Far East)), and India . . . . *M. crassicauda* Mordvilko

– Antenna usually with less than 20 secondary rhinaria on Ant.III, confined to basal half or ⅔ in a line. SIPH usually shorter than cauda, at most equal. On *Vicia* spp. (*cracca, faba, sativa* Linn.) and *Lathyrus* spp. (*pratensis* Linn, *montanus* Bernh.,). Europe, Central Asia, Middle East, Ethiopia . . . . *M. viciae* Buckton

4. SIPH pale, shorter (0.67–0.95×) than cauda. Ant.III with more than 10 secondry rhinaria. All legs pale except distal end of tibiae and tarsi pale brown. Processus terminalis (PT) 3.55–3.67× as long as base of Ant.VI. On *Lathyrus maritimus* Bigel. Northern Europe (Denmark, Sweden, Finland, Norway, Poland, northrn Germany) . . . . *M. litoralis* Müller

– SIPH dark brown or black, distinctly longer than cauda. Ant.III with fewer than 10 secondary rhinaria. Legs dark brown, at least fuscous on distal half of femur and tibiae. PT more than 4.5× as long as base of Ant.VI 5

5. URS 0.89–1.17× as long as 2HT, 0.68–0.88× Ant.VIb. Antennal tubercle weakly developed. Frons more than twice as wide as median depth. Antenna short, 0.83–0.94× as long as body length. SIPH 1.07–1.31× as long as Ant.III. On *Lespedeza* spp (*bicolor* Turcz., *cyrtobotrya* Miq.), *Cajanus cajan* Druce, *Desmodium trifolium* (L.) DC. East Asia (Korea, Japan, China, Taiwan), India, Swizerland (recently discovered by Giacalone and Lampel 1996) . . . . . *M. lespedezae* (Essig and Kuwana)

– URS 0.71–0.83× as long as 2HT, 0.47–0.54× Ant.VIb. Antennal tubercle well developed. Frons V-shaped, as wide as median depth. Antenna at least 1.3× as long as body length. SIPH shorter than Ant.III 6

6. Cauda short, 0.5× as long as SIPH. SIPH with narrow base, basal diameter shorter than middle diameter. Hairs on Ant.III 0.5× as long as basal width of Ant.III. On *Indigofera* (*dosua* Wall., *gerardiana* R. Grah., *teysmanni* Miq.), *Hedysarum campanulatum*. Indian Subregion (India, Pakistan, Afghanistan, Kashmir), and Thailand . . . . *M. dooarsis* (Ghosh and Raychaudhuri)

– Cauda elongated, more than 0.7× as long as SIPH. SIPH widest at base. Hairs on Ant.III very short, ¼× as long as basal width of Ant.III. On *Lespedeza bicolor*. Alate viviparous female unknown. Japan . . . . *M. brevipilosa* Miyazaki

Alate Viviparous Females

1. Cauda dark brown or black. On *Vicia* spp. or *Lathyrus* spp. 2

– Cauda pale yellow, at most fuscous. Not on *Vicia* spp. 4

2. Ultimate rostral segment (URS) as long as (0.93–1.17×) 2HT. Ant.I, mandibular laminae (ML), abdominal tergite III, and genital plate with 13–19, 6–8, 20–24, and 23–31 hairs respectively. Ant.III with 62–89 secondary rhinaria. Body entirely dark brown or black in life. Tibia pale yellow except extreme base and apical ⅕ in macerated specimens . . . . *M. nigra* Lee, n. sp.

– URS distinctly shorter (0.66–0.86×) than 2HT. Ant.I, ML, abdominal tergite III, and genital plate with fewer hairs, 9–15, 3–5, 15–22, and 16–24, respectively. Ant.III with relatively fewer secondary rhinaria (23–60). Body green except head and thorax including antenna, legs, siphunculi, and cauda black in life. Tibia black or dark brown in macerated specimens 3

3. Antenna with 46–64 secondary rhinaria on Ant.III. Ant.IV with 17–31 secondary rhinaria scattered throughout the segment. SIPH as long as or frequently longer (1.00–1.11×) than cauda . . . . *M. crassicauda* Mordvilko

- Antenna usually with less than 40 (23–38) secondary rhinaria on Ant.III. Ant.IV without or rarely 1–7 secondary rhinaria on basal ½ in a line. SIPH usually shorter (0.76–1.00×) than cauda . . . . *M. viciae* Buckton

4. SIPH pale, shorter (0.88–0.90×) than cauda. Ant.III with more than 30 (37–38) secondary rhinaria scattered throughout the segment. Ant.IV with 6–8 secondary rhinaria in a line. Processus terminalis (PT) 3.88–4.16× Ant.VIb . . . . *M. litoralis* Müller

– SIPH dark brown or black, distinctly longer (1.30–1.81×) than cauda. Ant.III with less than 15 secondary rhinaria in a line. Ant.IV without or rarely 1–2 secondary rhinaria. PT more than 5.0× Ant.VIb 5

5. SIPH 0.93–1.05× as long as Ant.III. Ant.III and Ant.IV with 10–15 and 1–2 secondary rhinaria respectively. URS as long as (0.93–1.09×) 2HT and 0.63–0.78× Ant.VIb. Antenna slightly longer (1.07–1.21×) than body length . . . . . *M. lespedezae* (Essig and Kuwana)

– SIPH distinctly shorter (0.64–0.66×) than Ant.III. Ant.III with 6–9 secondary rhinaria and Ant.IV without secondary rhinaria. URS distinctly shorter (0.67–0.84×) than 2HT and 0.45–0.50× as long as Ant.VIb. Antenna distinctly longer (1.50–1.70×) than body length . . . . *M. dooarsis* (Ghosh and Raychaudhuri)

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BIOLOGY, IMMATURE STAGES, AND REDESCRIPTIONS OF *HYDRELLIA PERSONATA* DEONIER (DIPTERA: EPHYDRIDAE), A *LEMNA* MINER

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Abstract.—*Hydrellia personata* Deonier (Diptera: Ephydridae) is a rarely collected shore fly found in the western and midwestern United States. We encountered a population in a constructed wetlands in southern California where the larvae were miners of duckweed (*Lemna minor* L.). Eggs were inserted between the upper and lower layers of epithelial tissue. Newly hatched larvae either bored into a duckweed thallus or separated the upper and lower epithelial layers to gain access to the photosynthetic tissue. Each instar mined several plants prior to molting inside of a plant thallus, and pupariation occurred inside a hollowed-out thallus. Several pupae were parasitized by the braconid *Cyrtogaster clavicornis* Walker. Overall, the biology and morphology of the immature stages were very similar to that of the closely related genus *Lemnaphila.* We describe all immature stages and redescribe the adult (male and female) based upon the newly collected materials. The unusual adult morphology of this species prevents its placement into any of the existing species groups of *Hydrellia.*

Key Words: shore flies, *Hydrellia,* aquatic insects, leaf miner, herbivory, duckweed, *Lemna,* wetlands

Shore flies (Diptera: Ephydridae) represent a species-rich family of acalyptrate Diptera with a world-wide distribution (Mathis and Zatwarnicki 1995). Most species are intimately linked to aquatic and semi-aquatic habitats, and this family displays vast adaptive radiation in larval feeding habits. Shore flies exploit detritus, bacteria, cyanobacteria, diatoms, green algae, plants, decaying animal carcasses, and prey on heterospecific invertebrates (Foote 1995). Although many shore flies are associated with aquatic macrophytes as secondary stem borers (e.g., Deonier 1999, Keiper et al. 2001) or use plant stands as refugia (Todd and Foote 1987, Keiper et al. 1998, Keiper and Walton 2000), the genera *Hydrellia* Robineau-Desvoidy, *Lemnaphila* Cresson, and *Cavatorella* Deonier represent the only known ephydrid leaf miners from aquatic habitats (Deonier 1998).

Duckweed (*Lemna minor* L.: Lemnaceae) is a characteristically minute plant whose mature individuals are 1–3 mm long and 0.5–1 mm wide (Mason 1957). Despite its small size, certain species of *Hydrellia* (Deonier 1998) and all *Lemnaphila* spp. (Scotland 1934, 1939; Mathis and Edmiston 2000) exploit duckweed as a host plant. The best studied examples of ephydrids associated with *Lemna* are *Lemnaphila scotlandae* Cresson and *Hydrellia williamsi* Cresson (Williams 1938, Scotland 1939, Mathis and Edmiston 2000). Larvae mine the photosynthetic tissues of multiple plants prior to pupariation, and puparia are formed within the last larval host plant. Mansor and Buckingham (1989) discussed the possible use of *L. scotlandae* in biocontrol efforts of large populations of duckweed and demonstrated its restricted host range using ovipositional and larval development studies.

During investigations of the distribution and abundance of Diptera in the Prado Constructed Wetlands (CA, Riverside Co.), we encountered mined duckweed plants containing puparia. *Lemnaphila scotlandae* and *H. griseola* (Fallén) (Grigarick 1959) were the only two previously known Nearctic miners of duckweed. The distribution of *L. scotlandae* is restricted to areas east of the Mississippi River (Mathis and Zatwarnicki 1995, Mathis and Edmiston 2000) and *H. griseola* is highly polyphagous (Deonier 1998). Adults reared from the duckweed plants proved to be *Hydrellia personata* Deonier (1971), a relatively rare species for which few specimens are available. We provide a redescription of the male and female based on the new material obtained, and describe the immature stages and general biology.

MATERIALS AND METHODS

The Prado Constructed Wetlands are a series of freshwater marshes interconnected by water control structures, encompass more than 125 ha, and are supplied with water from the Santa Ana River. The wetlands support a mosaic of emergent and submerged vegetation, most notably California bulrush (*Schoenoplectus californicus* [Meyer] Sojak), cattails (*Typha* spp.), lesser duckweed (*Lemna minor* L.), emergent and submerged species of buttercups (*Ranunculus* spp.), and pennywort (*Hydrocotyle ranunculoides* L.). Nearby aquatic habitats include periodically flooded duck club ponds and low gradient intermittent streams.

Immature specimens were collected by scooping up duckweed clusters with mosquito dippers. Samples were scanned with a dissecting microscope at 6–12× to find plants with eggs, larvae, or puparia. Specimens were reared in petri dishes, and active larvae were given undamaged plants to observe feeding. Plants with puparia were placed in petri dishes, kept at laboratory temperatures (18–20° C), and a 16:8 light: dark photoperiod maintained with incandescent lights. Representatives of all immature stages were fixed in KAA solution and preserved in 70% ethanol.

Field-collected adults were placed in breeding cages with marsh water and duckweed for observations of mating behavior, oviposition, and adult feeding. Small cages manufactured from plastic cups inverted on petri dishes were ineffective, as adults spent most of their time resting at the screened openings. Larger, 2 liter plastic boxes with screened lids seemed to provide a better adult habitat as the flies spent considerable time among the floating duckweed placed within. Breeding cages were exposed to the same photoperiod and temperature regime as larvae.

RESULTS AND DISCUSSION

The following adult description is based upon the original type series and 31 specimens collected by JBK, MS, JJ, and WEW at the Prado Constructed Wetlands, Riverside County, CA. For methods, indices, and other terminology see Deonier (1998).

Hydrellia personata Deonier
(Figs. 1–13)

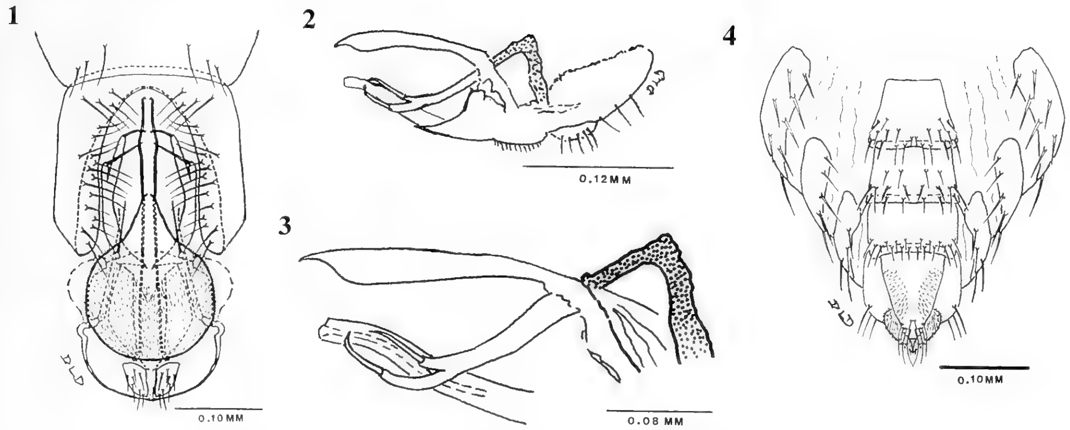
Hydrellia personata Deonier 1971: 86.—Mathis and Zatwarnicki 1995: 85.—Deonier 1998: 35, 42.

Diagnosis.—Maxillary palp dark brown, smoothly angular and slightly spathulate with 3–4 apical setae about 0.3+ of palpal length; 5–8 (usually 5–6) dorsal aristal rays; antenna dark brown (velvety in dorsal view); antennomere 3 with sparse (occasionally dense) light golden-brown micropubescence visible in dorsomedial view; frontal vitta and parafrontalia velvety dark-brown pruinose in dorsal view; antennomere 2 with usally 2 prominent spinoid apicodorsal setae; face, in profile with lower 0.5 slightly convex (not bulging) and with a slight median carina; face sericeous silvery or light-gray pruinose, contrasting with dark brown, narrow, unilinear parafacialia; 3–4 primary facial setae, with usually 1 minute upper secondary facial setula; ocular index 4.0–5.0; head width/head height 1.3–1.7; 1 postsutural (nearly sutural) dorsocentral macrochaeta present; pleuron densely olive- or reddish-brown pruinose; legs, except yellowish orange trochanters, tibial apices, and tarsal venters, dark brown; tibiae not dilated or expanded; mesonotal disc and abdomen semiglossy or glossy brown in dorsolateral view. Male length 1.28–1.80 mm; female 1.45–2.20 mm. Male postabdomen as in Figs. 1–3 and 5; female postabdomen as in Figs. 4 and 6.

Description.—*Head:* Face, in profile, with lower 0.5 slightly convex (not bulging) and with a slight, but noticeable median carina; face sericeous silvery or light-gray pruinose, contrasting with dark-brown, narrow, unilinear parafacialia; antennal foveae indistinct; epistoma squarely recessed (sometimes slightly concave with median indentation) and congruent with dark brown anteclypeus; 3–4 primary facial setae in 1 row, with 1–3 (usually 1) minute, porrect or declinate secondary facial setulae; antenna dark brown (velvety in dorsal view); antennomere 2 with usually 2 prominent, spinoid apicodorsal setae; antennomere 3 with sparse (occasionally dense) light golden-brown micropubescence visible in dorsomedial view; 5–8 (usually 5–6) dorsal aristal rays; frontal vitta and parafrontale often scarcely differentiated, both appearing velvety dark-brown pruinose in dorsal view (except ocellar triangle sometimes light-brown pruinose); fronto-orbital area concolorous with parafrontale; anterior fronto-orbital seta 0.3–0.5 length of posterior seta; frons moderately sloping; 12–16 postocular setae in fairly regular row nearest posterior orbit; maxillary palpus dark brown, smoothly angular and slightly spathulate with 3–4 apical setae about 0.3+ of palpal length. Epistomal index 1.0–1.4; mesofacial index 1.5–2.0; vertex index 5.5–7.0; ocular index 4.0–5.0; subcranial index 1.3–2.0; head width/head height 1.3–1.7.

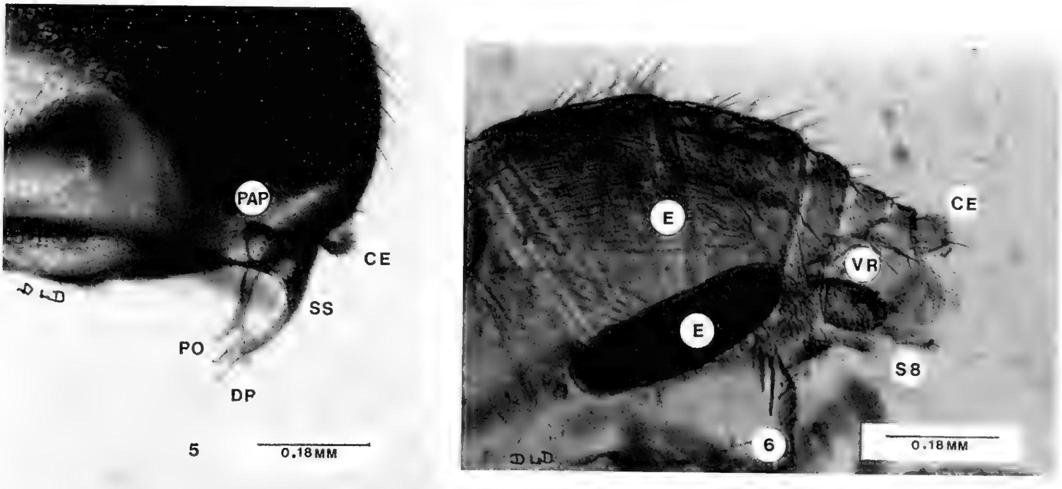
Thorax: Postpronotum and notopleuron usually densely olive-brown pruinose, but sometimes dark-brown or light yellowish-brown pruinose; mesontal disc, in dorsolateral view, glossy dark brown with sparse to moderately dense olive-brown pruinosity; 3–4 antesutural (1–2 × macrochaetous) and 1 postsutural (macrochaetous) dorsocentral setae [Riverside Co. CA population with only postsutural (nearly sutural) dorsocentral seta macrochaetous]; minute, paired auxiliary apical scutellar setulae usually present between apical scutellar macrochaetae; pleuron usually concolorous with notopleuron, but sometimes moderate reddish-brown pruinose; 1 mesokatepisternal seta (macrochaetous); legs, except yellowish orange trochanters, apical 0.2 of tibiae, and tarsal venters, dark brown with sparse to moderately dense olive-brown pruinosity; meso- and metatibiae not dilated or expanded. Wing lenth 1.25–2.04 mm; veins dark brown; 6–8 setae on basal end of costa; 3–6 dorsal and 6–9 anterior interfractural cotal setae; costal-section ratios: II: I 1.8–2.2; III: IV 3.5–4.0; V: IV 3.0–3.6; M_{1+2} index 1.2–1.5.

Abdomen: Terga dark brown with sparse to moderately dense light-brown pruinosity in lateral view, but glossy or semiglossy in dorsolateral and posterodorsal views. Male postabdomen: median 0.3 of sternum 5 broadly concave; anterolateral margin of sternum 5 rounded through 95°–100° angle; copulobus truncate to diagonally truncate posteriorly and somewhat irregularly setose. Postgonite bifurcate and paralleling distiphallus for over 0.5 latter's length; median branch 2.0–2.5× length of lateral branch of postgonite and with slightly curved postgonite uncus about 0.5 length of



Figs. 1–4. *Hydrellia personata.* 1, Male genitalia, ventral view. 2, Male genitalia, left lateral view. 3, Male genitalia emphasizing phallapodeme, bifurcate postgonite, and distiphallus, left lateral view. 4, Female postabdomen, ventral view.

more nearly straight uncus of lateral branch; both postgonite unci directed mediad toward distiphallus; pregonite much smaller, straight, and covered by fused surstyli; distiphallus long, digitiform, and often slightly expanded at midlength, upcurved and slightly tapering to nearly blunt apex in lateral view; basiphallus concealed in ventral view by fused surstyli (in cleared specimens appearing as slightly wider continuation of distiphallus); phallapodeme, in lateral view, darkly sclerotized and forming right angle above basiphallus, but showing no distinct condylar scar or process. Fused surstyli with nonpubescent, acute, anteromedial papilliform projection and with single (paired) anteriorly projecting macrochaeta inserted anterolaterally; fused surstyli length:cercus length (ventral view) about 4.8:1.0. Epandrium (syntergum 9+10)



Figs. 5–6. *Hydrellia personata.* 5, Photomicrograph of male postabdomen with exserted genitalia, left lateral view. 6, Photomicrograph of female postabdomen (partly cleared), left lateral view. Abbreviations: CE, cercus; DP, distiphallus; E, egg; PAP, phallapodeme; PO, postgonite; SS, surstyli; S8, sternum 8; VR, ventral receptacle.

evenly rounded (semicircular) posteriorly. Female postabdomen: sternum 8 slightly narrower basally than 7, about 1.5× longer than wide, and tapering conically posteriad; tip of sternum 8 with 6–8 long, slightly incurved setae arranged in a semirosette in ventral view; sterna 6 and 7 nearly quadrangular, 5 noticeable wider distally than basally; cercus, in lateral view, diagonally to roundly truncate distally, 1.2–1.4× as long as wide, and directed straight posteriad. Ventral receptacle cupuliform, about 1.5× deeper than wide.

Types.—*Hydrellia personata* Deonier 1971: 86 [USA. Washington. Grand: O'Sullivan Dam; HT ♂, Washington State University (322)]; 1998: 35, 42 [revision].—Mathis and Zatwarnicki 1995: 85 [world catalog].

Additional specimens examined.—California: Riverside County, Prado Wetlands, pan trap (VII-2-1999, coll: J. B. Keiper), 3 ♂, 2 ♀; (VII-10-1999, collector: J. B. Keiper), 1 ♂, 3 ♀; (V-4-2000, collector: J. B. Keiper) 4 ♂, 18 ♀ (1 ♂ in Deonier Collection, remainder in collection of Cleveland Museum of Natural History).

Distribution.—Found from Washington to southern California, east to Iowa and Texas.

Remarks.—The identification of pregonite and postgonite was erroneously reversed in the original description. DLD has still not been able to place this species in a species-group. It differs from the *H. prudens* and *H. tibialis* species-groups noticeably by its wide head, and its normal, unexpanded male mesotibia. For the original type-series, the only habitats recorded were sedge meadow and margin of Mono Lake, California.

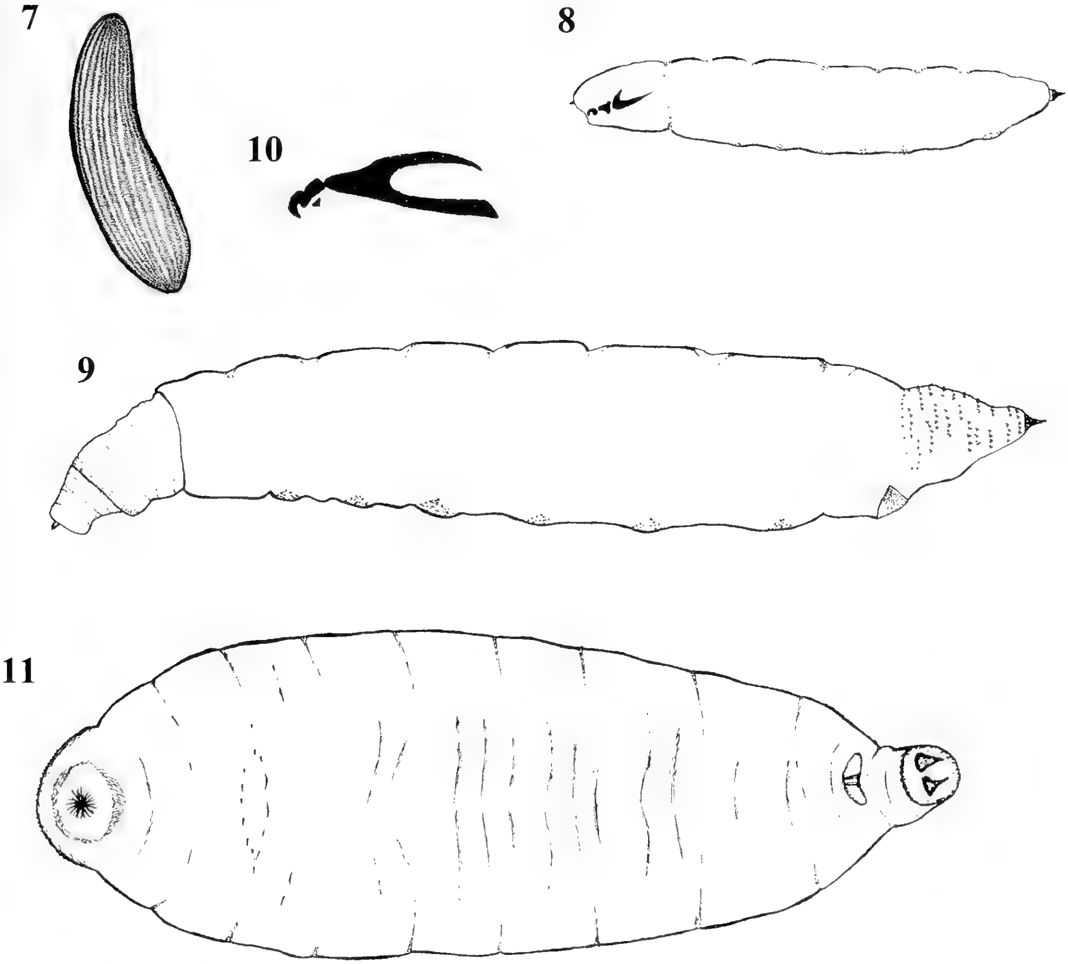
Immature stages.—*Egg* (n = 5): Length, 0.36–0.38 mm ($\bar{x}$ = 0.37). White, ends bluntly rounded, with longitudinal ridges along entire length; ridges interconnected with narrow cross ridges. Micropyle small and inconspicuous (Fig. 7).

First instar (n = 2): Similar to third instar except in the following: Length, 0.87–0.89 mm ($\bar{x}$ = 0.88); maximum width, 0.14–0.15 mm ($\bar{x}$ = 0.15). Body white, somewhat transparent; little distinction among abdominal and cephalic segments. Cephalopharyngeal skeleton reduced, especially dorsal cornu. Breathing tube lacking spines (Fig. 8).

Second instar (n = 6): Similar to third instar except in the following: Length, 1.13–1.65 mm ($\bar{x}$ = 1.40); maximum width, 0.20–0.32 mm ($\bar{x}$ = 0.26). Body nearly opaque yellowish; little distinction among abdominal and cephalic segments. Cephalopharyngeal skeleton somewhat reduced. Breathing tube with minute brown spines only.

Third instar (n = 7): Elongate, muscoid (Fig. 9). Maximum length, 2.24–2.77 mm ($\bar{x}$ = 2.47); maximum width, 0.43–0.53 mm ($\bar{x}$ = 0.47); widest at approximately posterior 2/3; yellow in life, fading to opaque white in preservative. Short antennae anteriorly, dark brown; facial mask generally triangular, with median carina (Fig. 12). Pseudocephalic segment lined with rows of narrow, minute spines that increase in length posteriorly; anterior spines approximately 0.2× length of longest posteior spines. Anterior spiracles absent. Abdominal segments well-defined; anterior abdominal segments not strongly adorned, posterior segments adorned with 9–10 rows of short brown spines dorsally; breathing tube short, representing <1/10 of total body length, lacking spines; posterior spiracles tipped with brown conical spines ~0.04 mm long, each spine bordered by 4 palmate groups of hydrofuge hairs (Fig. 13); abdominal segments 2–7 with fleshy ventral creeping welts adorned with fine spinules; perianal pad oblate, tapering laterad, ~0.15 mm wide. Cephalopharyngeal skeleton typical of *Hydrellia*; mouthhook strongly curved, no accessory teeth; dental sclerite small and triangular; dorsal cornu tapering posteriorly, posterior cornu truncate posteriorly, both lacking windows (Fig. 10).

Puparium (n = 17): Length, 1.52–2.16 mm ($\bar{x}$ = 1.91); maximum width, 0.63–0.94

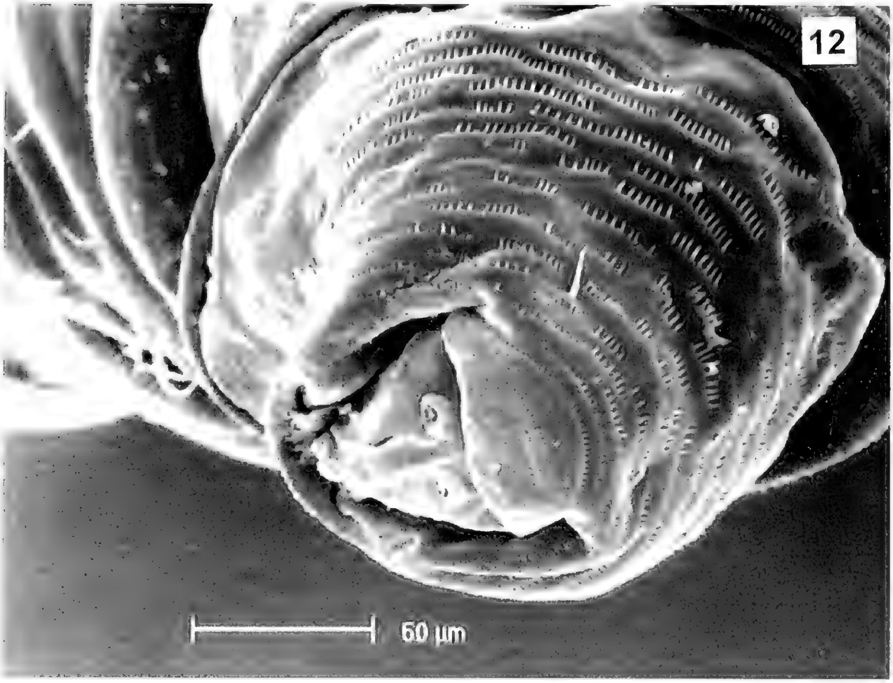


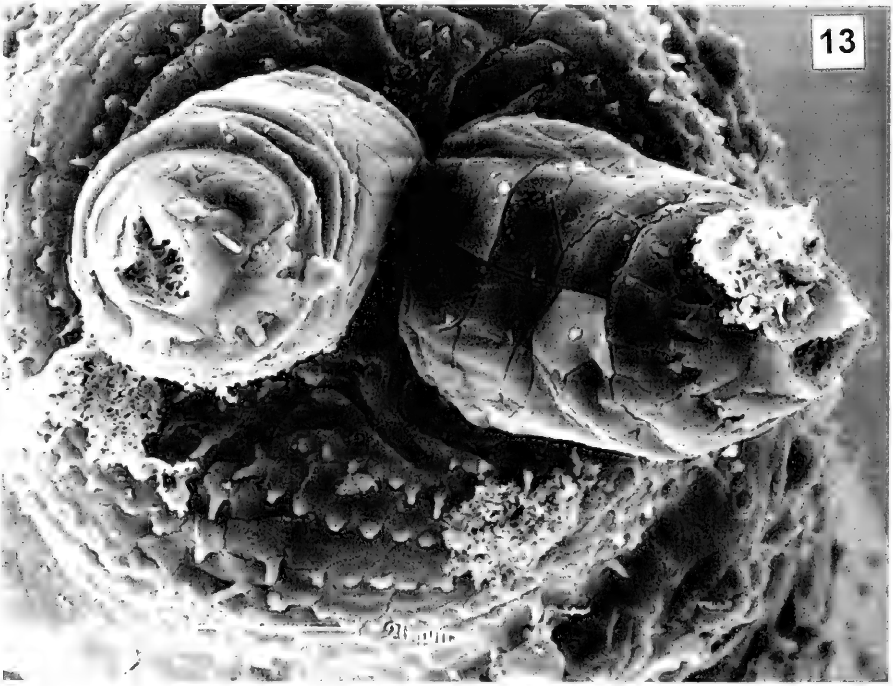
Figs. 7–11. *Hydrellia personata.* 7, Egg, dorsal view. 8, First instar, lateral view. 9, Third instar, lateral view. 10, Same, cephalopharyngeal skeleton. 11, Puparium, ventral view.

mm ($\bar{x}$ = 0.74). Amber; segmentation conspicuous, margin of puparium smooth; broadly rounded anteriorly, tapering posteriorly, widest anteromedially. Posterior spiracles dark, curved ventrad (Fig. 11). Third instar cephalopharangeal skeleton pressed flat, visible through puparium.

Remarks.—The eggs of *H. personata* are easily distinguished from those of *L. scotlandae* (Mathis and Edmiston 2000). Those of *L. scotlandae* are flattened ventrally, have only four longitudinal ridges, and have a light brown chorion, whereas those of *H. personata* are not flattened, have more than 4 longitudinal ridges, and the chorion is white. In contrast, the mature larvae are very similar in these two *Lemna*-consuming species, including the general shape, ventral creeping welts, conical posterior spiracles, and morphology of the mouth-hooks of the cephalopharyngeal skeleton. A slight difference exists in the puparia, as *L. scotlandae* are widest posteromedially and *H. personata* are widest anteromedially.

Biology and larval feeding habits.—Adults of *H. personata,* some of the smallest in the genus, have been collected in five states from the Pacific coast to the Mississippi River. This distribution is entirely within the distributional range of the now





Figs. 12–13. *Hydrellia personata.* 12, Scanning electron micrograph of third instar facial mask. 13, Same, posterior spiracles.

known single larval host-plant species, *Lemna minor* L. Although this host-plant species has now been confirmed through rearings, much remains unknown about the natural history of this rare little *Hydrellia.* Despite records of populations in Iowa and Texas, prolonged surveys with floating adhesive traps or floating detergent traps by DLD on the many year-round *Lemna* pools in southeastern Kansas have failed to discover its presence there. Many *L. scotlandae* (over 100) and a few *H. griseola* and *H. bilobifera* Cresson along with four *Setacera* sp. and one *Discocerina obscurella* (Fallén) were the only ephydrids trapped.

Adult populations of the Prado Constructed Wetlands were located only in areas of dense duckweed growth (at least three plants cm^{-2}), where they were observed walking or resting on duckweed plants. Some areas of the wetlands with dense growths harbored no adults (or evidence of immatures), whereas other areas supported flies in abundance. Their small size and habit of walking on duckweed plants allowed us to observe adults or capture them with vials easily. Although adults exhibited the capacity to skate on the water surface, they did so only rarely and appeared to prefer the solid substrate offered by the floating plants. Adults fed by sponging the dorsal surface of duckweed plants with their mouthparts and sometimes touched their probosci to the water surface. Unlike *L. scotlandae* adults (Scotland 1934, Mathis and Edmiston 2000), *H. personata* did not appear to damage the plants.

Flies moved slowly over the surface of thick growths of duckweed, and flew short distances if disturbed. Intraspecific aggression was apparent when conspecifics wandered closely (approximately 1–1.5 cm) to a stationary female. The female would rapidly approach the intruder causing it to retreat. Males did not display aggressive behavior during our observations.

Eggs were infrequently collected in nature, and only one egg was laid during laboratory observations. All eggs were inserted about half way into the peripheral margin of duckweed plants and positioned so the micropylar end protruded freely from the plant. Three to four eggs, situated adjacent to each other, were inserted into each of five field-collected plants; the single egg laid in the laboratory was placed similarly.

The small size of the immatures made it impossible to locate them in nature. However, population sizes were large enough that scooping duckweed from between stems of emergent plants produced ample specimens for study and rearing. Newly hatched larvae burrowed into the host plant or stretched their bodies and probed the surrounding area until a neighboring plant was located. Larvae latched onto the nearby plant with their mouthhooks and pulled themselves onto the new host. Older larvae used their mouthparts to separate the dorsal and ventral halves of plant fronds and fed on the exposed photosynthetic tissues. Larvae crawled into the hollowed area of the plant as tissue was removed. The posterior spiracles remained outside of the plant and in contact with the atmosphere. Two first instars did not separate the dorsal and ventral halves of the host frond, but moved to the underside of the plant where they burrowed through the epithelial tissue to gain access to the photosynthetic tissues. Young larvae did not hollow plants completely, but created U-shaped mines prior to exiting and moving to another host plant. Conversely, second and third instars always attacked plants by separating the two halves of the frond and consuming all the photosynthetic tissues or nearly so.

Molting occurred inside duckweed plants and exuviae remained within the hosts. Puparia were formed within hollowed-out duckweed fronds, but the posterior spiracles did not extend to the atmosphere. Damaged duckweed plants remained floating on the water surface, and atmospheric air probably diffused into the damaged plant through the epithelial break formed by third instars. Adults exited plants through the epithelial break. Five adult *Cyrtogaster clavicornis*

Walker (Hymenoptera: Braconidae) (2f, 7 Oct 1998; 3f, 9–15 Jan 2000) emerged from field-collected puparia situated within duckweed plants. This parasitoid has also been reared from puparia of *H. griseola* (Fulmek 1962).

Because of difficulty with laboratory rearings and the intimate trophic association of *H. personata* with duckweed in nature, the precopulation period, fecundity, and seasonal distribution remain unknown. The first specimens collected were puparia taken 22 September 1998, and further larvae and puparia were collected 26 September 1998 and 29 June 1999 for rearing. Adults were observed during January 2000, and puparia within plants were collected among a senescing population of duckweed at that time. No larvae or eggs were found during the winter months. Sporadic collections of adults and all immature stages indicate that *H. personata* is multivoltine and exhibits many overlapping generations in the latitude of southern California. The first, second, and third larval stadia were 2–3, 2–3, and 4–5 days, respectively, with a pupal duration of 8 days.

The control certain of pestiferous aquatic plants using dipterans has been successful (Center et al. 1997), and has been tested for *Lemna* (Mansor and Buckingham 1989). Although biocontrol programs against large blooms of duckweed have not been implemented rigorously, *Hydrellia personata* represents such an opportunity. Biocontrol efforts with this shore fly in the western United States may allow for use of a local species rather than having to import an exotic one from a geographically distant area.

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HAMLET CLARK: PUBLICATIONS AND PROPOSED TAXA

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Abstract.—Hamlet Clark (1823–1867) was an English cleric who was interested in natural history. He became an authority on the Chrysomelidae, Dytiscidae, Gyrinidae, Haliplidae, and Noteridae (Coleoptera). From 1842 until 1867 he published 39 papers in which he described 71 genera and 709 species. This article presents a brief biographical sketch, a bibliography of his published works, and a list of proposed taxa.

Key Words: Clark, biography, bibliography, proposed taxa

BIOGRAPHICAL SKETCH

The information summarized below was taken from the obituaries of Clark (Anonymous 1867; Newman 1867a, b, c; and Clark's articles 14 and 35).

Hamlet Clark was born 30 March 1823 in Navenby, Lincolnshire, England. He was the eldest son of Rev. Henry Clark, Vicar of Harmston, Lincoln. He attended Beverly Grammar School and then studied with the Rev. Mr. Scott where he first became interested in natural history. Clark was a sick child and as a result he was unable to participate in many activities.

Clark attended Corpus Christi College at Cambridge University and was a student with the the Coleopterist T. Vernon Wollaston (Jesus College). Cambridge at this time did not offer much formal training in natural history, but Clark read much natural history and purchased many natural history specimens from residents in the Cambridge area.

Clark's early natural history interests were birds, spiders, and Lepidoptera. He devoted the last ten years of his life to the study of Coleoptera, especially water beetles and leaf beetles.

Clark traveled and collected throughout Great Britain. In the spring of 1856 he took a two month cruise on John Edward Gray's (Lepidopterist and explorer from the British Museum) yacht visiting many localities in Spain and Algeria. In December of the same year he traveled to Rio de Janeiro, Brazil also with Gray. While in Brazil he collected at Corcovardo Mountain, Pijica (just north of Rio), Constancia, Presidencia (in the Organ Mountains), and Paraihiba.

Clark became a fellow of the Entomological Society of London in 1850. He served on the council in 1864–5 and as Vice President in 1864. Clark attended and participated in many Society meetings when he was in London. He became a fellow of the Linnean Society of London on 21 June 1860.

Clark was described as tall and handsome with a friendly outgoing personality. He served as curate of All Saints Parish in Northampton from 1848 until 1856, and he was conscientious in his ministerial duties. From 1856 to 1863 he lived in London. Due to poor health he left the ministry in 1863. Most of his private journals, field notes, and manuscript notes were destroyed "due to a most untoward accident" prior to his death. At the time of his death he was engaged in working on a catalog of the Hydradephaga for the British Museum. He died 10 June 1867 at Rhyl, Wales, and is buried in the Rhyl Cemetery.

Clark's British Coleoptera and Lepidoptera were sold at auction in 1865 by J. C. Stevens. His Elateridae, Hydradephaga, and Phytophaga were sold to a Mr. Higgins and were deposited in The Natural History Museum, London, in 1867. Clark's material was accessioned as number 67-56 and most specimens from the collection should bear a label with this number.

ANALYSIS OF CLARK'S PROPOSED TAXA

One measure of the value of a taxonomist's work is how proposed taxa have been accepted by other scientists. In 39 publications Clark proposed 71 genus group names and 709 species group names. Of the 71 generic names, 17 (23.9%) are now synonyms and 6 (8.5%) are homonyms (Seeno and Wilcox 1982). The 23 names represent 32.4% of the names proposed.

The species group names were analyzed using the most recent catalogs on each group (Blackwelder 1946; Clavareau 1914; Heikertinger and Csiki 1939, 1940; Jolivet 1971; Monrós 1958, 1959; Weise 1916; Wilcox 1971, 1973; Zimmermann 1920). Of the 709 names proposed, 74 (10.4%) are synonyms and 7 (1%) are homonyms. These 81 names represent 11.4% of the taxa proposed.

Clark's rate of unacceptable names is very high, especially at the generic level. This level of invalid names is fairly normal for a worker who described species rather than doing revisionary work. Many of the genera containing Clark species group names have not been revised since his death, so the percentage of unacceptable names may rise.

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3b. 1845. *Omaseus aterrimus.* Zoologist (1)3: 1,016.
3c. 1845. *Mesosa nubia.* Zoologist (1)3: 1,016.
3d. 1845. Captures in the Cambridge fens. Zoologist (1)3: 1,016.
3d. 1845. Scarcity of certain Dytiscidae. Zoologist (1)3: 1,016.
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TAXA PROPOSED BY CLARK

Taxa are listed alphabetically by genus under each higher taxonomic catagory; the numbers are the publication number followed by the page number.

Class Arachinda
Order Araneida
Salticidae

Salticus blackwalli 8: 329

Class Insecta
Order Coleoptera
Chrysomelidae

Alticinae

Aedmon 16: 129
Aedmon sericellum 16: 131
Allochroma 16: 181
Allochroma assimile 16: 191
Allochroma balii 16: 187
Allochroma coccineum 16: 184
Allochroma fasciatum 16: 186
Allochroma festivum 16: 192
Allochroma flavovittatum 16: 188
Allochroma generosum 16: 194
Allochroma humerale 16: 183
Allochroma lunatum 16: 188
Allochroma nigromarginatum 16: 190
Allochroma piceum 16: 184
Allochroma quatuorpustulatum 16: 191
Allochroma sexmaculatum 16: 185
Allochroma sexsignatum 16: 193
Allochroma venustum 16: 189
Apalotrius 16: 166
Apalotrius pubescens 16: 168
Argopus angulicollis 26: 148
Asphaera decipiens 32: 380
Asphaera fallax 32: 380
Asphaera marginata 32: 380
Asphaera subfasciata 32: 380
Aspicela 32: 378
Aspicela balyii 32: 381
Aspicela discoidalis 32: 381
Atyphus 16: 175
Atyphus carbonarius 16: 176
Atyphus comes 16: 177
Atyphus flaviventris 16: 177
Atyphus furcipes 16: 178
Cacoscelis bicolorata 32: 408
Cacoscelis clythraefromis 32: 407
Cacoscelis coeruleipennis 32: 407 [homonym, replaced by *coerulea* Csiki 1939]
Cacoscelis feldneri 32: 406
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THE STEM-BORING SAWFLY GENUS *CEPHUS* LATREILLE (HYMENOPTERA: CEPHIDAE) IN JAPAN

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Abstract.—Two species of *Cephus* occur in Japan, *C. hyalinatus* Konow from Hokkaido and *C. brachycercus* Thomson, newly recorded from Japan, from Honshu. Clarification of past records of *Cephus* in Japan are presented. A key, descriptions, and illustrations of the abdomen are given for both species.

Key Words: stem-borers, Cephidae, *Cephus,* Japan

Cephus is primarily a Eurasian genus of 20 to 25 species, all of which are associated with grasses. Gussakovskij (1935) keyed and discussed 23 Palearctic species, Benson (1946) estimated 25 world species, and Muche (1981) keyed and discussed 31 world species. Two species occur in North America, but one, *Cephus pygmaeus* (L.) is an introduction, and the other, *Cephus cinctus* Norton, is still open to question as to whether it is native or an early introduction from eastern Asia. Larvae bore and feed in the stems of grasses and can be especially destructive in cultivated grain crops such as wheat.

Takeuchi (1938) recorded four species of *Cephus* from northeastern Asia, but two of them, *C. nigripennis* Takeuchi and *C. sachalinensis* Takeuchi, are now placed in *Calameuta* Konow (Benson 1946). Of the other two, one, *Cephus hyalinatus* Konow, is known from eastern Asia including Japan (Hokkaido), and the other, *C. camtschatcalis* Enslin, from Kamtchatka and Sakhalin. Takeuchi (1938) corrected his previous record of *Cephus camtschatcalis* Enslin from Hokkaido (Takeuchi 1936) to *Cephus hyalinatus*. Takeuchi later recorded *C. camtschatcalis* from Kunashiri Island, but this is corrected to *C. hyalinatus* in this paper. Togashi (1997, 1998) gave collection records of *Cephus hyalinatus* from Akan, Hokkaido, and Niigata Prefecture, Honshu, respectively, but the latter was corrected to *Stenocephus oncogaster* Shinohara by Shinohara (1999).

Specimens of this genus are not commonly collected in Japan, and only a few from Hokkaido and Honshu are represented in collections. Based on about 35 specimens available, we record two species from Japan, *Cephus hyalinatus* from Hokkaido and *Cephus brachycercus* Thomson from Honshu. The former is widespread in eastern Asia, and the latter is widespread in Eurasia and is reported here for the first time from Japan. Based on the specimens available, there are rather constant color differences between those collected in Honshu and those from Hokkaido. Thus, at present we prefer to treat them as separate species, and we attempt to clarify past records from Japan.

Cephus belongs to the tribe Cephini, all of which are associated with grasses. It is separated from the other two genera of the tribe, *Calameuta* and *Trachelus,* by the following: Distance between antennae subequal to distance between antenna and tentorium; female sheath in dorsal view not broadened toward apex; male eighth sternite without concavity, with only a patch and apical fringe of modified flattened setae. In *Calameuta,* the distance between the antennae is much shorter than the distance between the antenna and tentorium (as 1.0: 1.5 to 2.0), and in *Trachelus* the female sheath is broadened at its apex and the male eighth sternite has a deep concavity with modified setae.

KEY TO JAPANESE SPECIES OF *CEPHUS*

1\. Female 2
– Male 3
2\. Abdomen (Fig. 1) with lateral yellow spots on segments 3–7, appearing almost as a lateral yellow longitudinal stripe, yellow transverse bands on posterior margins of abdominal segments 4 and 6, apex of 9th tergite broadly yellow; wings commonly moderately infuscated . . . . *hyalinatus* Konow
– Abdomen (Fig. 2) with lateral yellow spots on segments 3 or 4–7, spots small and separated, not appearing as a lateral longitudinal stripe, without yellow transverse bands, though 6th segment sometimes with narrow incomplete band on posterior margin, 9th tergite narrowly yellow at apex; wings hyaline . . . . *brachycercus* Thomson
3\. Abdomen (Fig. 3) with transverse yellow bands on posterior margins of segments 3, 4, 6, and 7, narrow or incomplete on 3 and 7, segments 3 or 4–7 with lateral yellow spots, sometimes minute spots on 2 and 8; wings commonly moderately infuscated; venter of cervical sclerite usually with yellow spot; mesepisternum with yellow spot on extreme upper corner and yellow spot usually on lower anterior area . . . . *hyalinatus* Konow
– Abdomen (Fig. 4) with transverse yellow bands on posterior margins of segments 4 and 6, lateral yellow spots on segments 3 or 4–7; wings hyaline; cervical sclerites and mesepisternum usually black except sometimes inner ventral surface of cervical sclerite with yellow spot and possibly a small yellow spot on dorsal corner of mesepisternum . . . . *brachycercus* Thomson

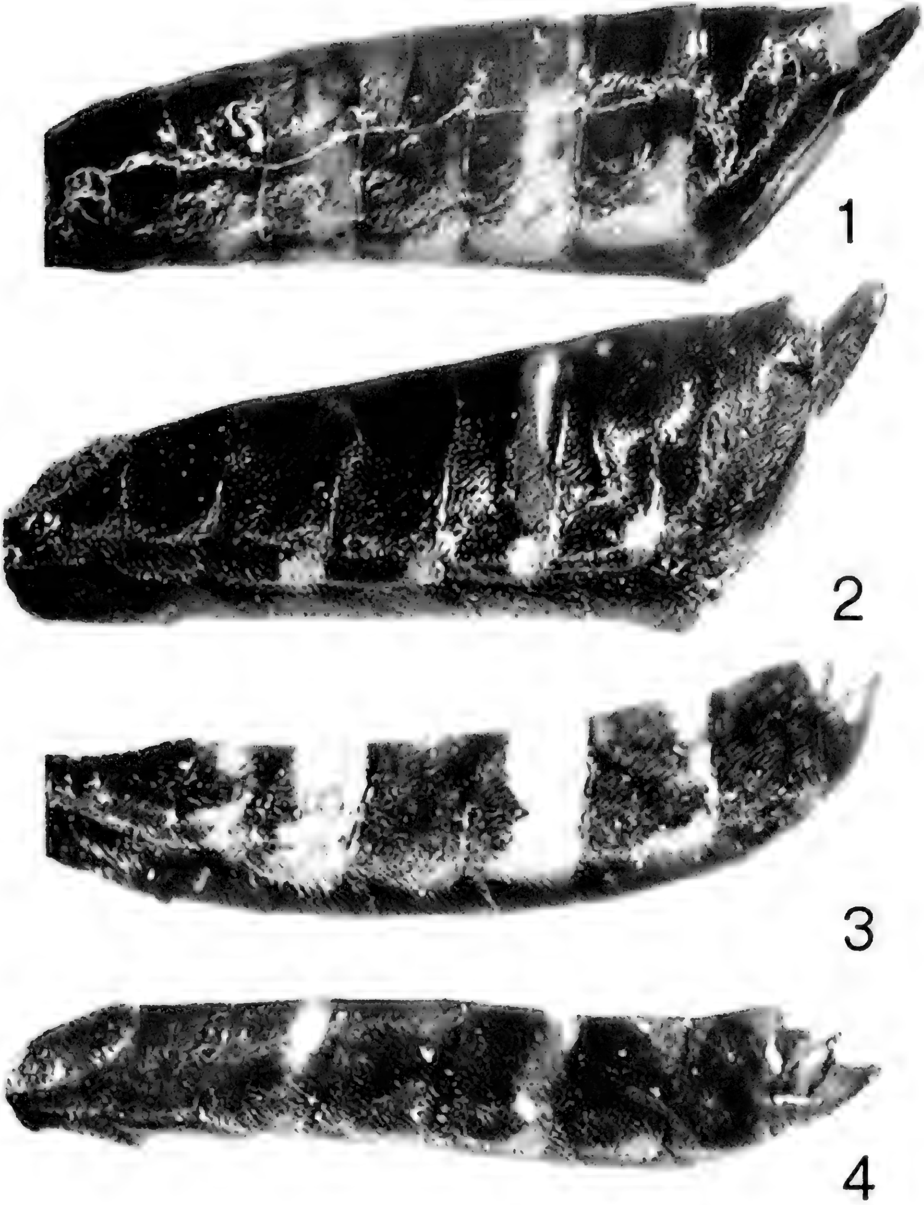
Cephus hyalinatus Konow
(Figs. 1, 3)

Cephus hyalinatus Konow 1897: 173.—Takeuchi 1938: (Hokkaido).—Togashi 1997: (Hokkaido).
Cephus camtschatcalis: Takeuchi 1936: 59.—Takeuchi 1955: 9 (misidentifications).

This species was described from "Sibiria or. (Irkutsk)." It has been recorded from various localities in eastern Russia (Gussakovskij 1935, Verzhutskii 1966), Kunashiri Island (Takeuchi 1955 [as *C. camtschatcalis*]), and Hokkaido, Japan (Takeuchi 1936 [as *C. camtschatcalis*]), Takeuchi 1938).

Female.—Length, 9.0–11.0 mm. Antenna and head black; mandible yellow with apex reddish brown; maxillary palpal segments 3–6 yellow. Thorax black, sometimes extreme upper corner of mesepisternum with small yellow spot. Fore- and midlegs black with tibiae and tarsi yellow. Hindleg black with tibia yellow with about apical fourth black. Abdomen black with segments 3–7 yellow laterally, yellow extending width of segments, thus appearing as a lateral longitudinal stripe; transverse yellow bands on posterior margins of segments 4 and 6; apex of 9th tergite broadly yellow. Oblong plate (valvifer 2) yellow ventrally. Wings moderately, uniformly infuscated; costa and anterior margin of stigma yellowish, rest of stigma and veins black. Antenna with 18 or 19 segments; preapical segments slightly longer than broad. Hindtibia with 2 preapical spines. Tarsal claw with a minute inner tooth, much shorter than outer tooth.

Male.—Length, 8.0–9.5 mm. Outer surface of antenna from segment 5 to apex yellowish. Head black, usually with yellow spot on lower inner orbit near malar area and spot on supraclypeal area bordering clypeus; these spots sometimes small or absent. Thorax black with yellow spot on extreme upper corner of mesepisternum; perapterum yellow; yellow spot on lower anterior mesepisternum, and yellow spot on



Figs. 1–4. Abdomen, lateral view. 1, *Cephus hyalinatus,* female. 2, *C. brachycercus,* female. 3, *C. hyalinatus,* male. 4, *C. brachycercus,* male.

venter of cervical sclerite. Fore- and midlegs with coxae yellow anteriorly, black posteriorly; trochanters black; outside margin of femora black, inside margin of femora and tibiae and tarsi yellow; hindleg similar but black mainly at base of coxa with apical half or more yellow. Abdomen black with lateral yellow spots on segments 3 or 4–7, sometimes minute spots on 2 and 8, spots separated; yellow transverse bands on posterior margins of segments 3, 4, 6, and 7, usually narrower on 3 and sometimes incomplete on 3 and 7. Apex of hypandrium and harpes of male genitalia yellow.

Japan records.—Hokkaido: Wakkanai, 7-VII-1977, col. K. Baba (2 ♀, 3 ♂); same except 5-VII-1977 (1 ♂); Rishiri Is., 2-VII-1968, T. Naito leg. (2 ♀, 1 ♂); Kawayu, 25-VI-1969, T. Naito (1 ♂); Teshio, 2-VII-1930, Takeuchi (identified as *C. hyalinatus* by Takeuchi) (1 ♂).

Other specimens examined.—Russia, Sakhalin: Konuma, 7-VII-1930 (identified as *C. hyalinatus* by Takeuchi) (2 ♀); Karafuto (= Sakhalin), 1922, coll. M. Yano ("753" K. Sato Collection 1975) (2 ♀); Sakhalin, Yuzhno-Sakhalinst City, meadows near forest stream, 15-VI-1971, V. Ermolenko (3 ♂); Sakhalin, Shenbunino Vil., meadow along Japanese Sea, 19-VI-1971, V. Ermolenko (1 ♀, 1 ♂). Russia, Primorski Kray, Primorskoe Vil., Reserve Kedzovaya "Padj", 11-VI-1966, G. Anufriev (1 ♂). Kuriles, Kunashiri, Yambetsu, 22–25-VII-1935, T. Uchida (1 ♀, 5 ♂); Etorofu, Porosu 14–15-VII-1936 (2 ♂), Seseki 16–18-VII-1936, Y. Sugihara (1 ♀) (identified as *C. camtschatcalis* by Takeuchi). Kunishir Island, Alekhino Vil., wet meadow along forest stream, 27-VI-1971, V. Ermolenko (2 ♂). Shikotan Island, Krabozavodsk Vil., meadows along Pacific Ocean, on flower of *Ranunculus* sp., 6-VII-1071, V. Ermolenko (7 ♀, 4 ♂). Shikotan Island, Malo-Kuril'sk Vil., meadows along Pacific Ocean, 9-VII-1971, V. Ermolenko (1 ♂).

Remarks.—Ivie and Zinovjev (1996) synonymized *C. hyalinatus* under *Cephus cinctus* Norton 1872 described from North America; thus, concluding that the same species occurs in Asia and North America and that the North American populations may have been the result of an early introduction from Asia. This synonymy is still open to question, and we prefer to call the Japanese specimens *C. hyalinatus* pending additional proof for the synonymy.

This species was recorded from Hokkaido by Takeuchi (1936, 1938), the latter reference correcting his 1936 identification of *C. camtschatcalis* to *C. hyalinatus*. We have seen the specimen on which Takeuchi based this record and confirm his identification as *C. hyalinatus*. Takeuchi (1955) recorded *C. camtschatcalis* from Kunishiri Island. We have examined those specimens, deposited in Hokkaido University, Sapporo, and confirm that they are actually *C. hyalinatus*. Togashi's (1998) record of *C. hyalinatus* from Honshu was erroneous and is actually *Stenocephus oncogaster* (Shinohara 1999).

Cephus brachycercus Thomson
(Figs. 2, 4)

Cephus brachycercus Thomson 1871: 322.

This species was described from Europe, but it occurs across the Palearctic (Gussakovskij 1935, Verzhutskii 1966) and is here newly recorded from Honshu, Japan.

Female.—Length, 6.5–8.3 mm. Antenna and head black; mandible yellow with apex reddish brown. Thorax black. Fore- and midlegs black with tibiae and tarsi yellow; hindleg black with tibiae yellow except for black on about apical fourth. Abdomen black with small lateral spots on segments 3 or 4–7, spots small and separated; sometimes a narrow, incomplete yellow transverse band on posterior margin of segment 6; apex of 9th tergite narrowly yellow. Oblong plate (valvifer 2) narrowly yellow on margin. Wings hyaline; costa and anterior margin of stigma yellowish, rest of stigma and veins black. Antenna with 18 to 22 segments; preapical segments about as broad as long. Hindtibia with 2 preapical spines. Tarsal claw with small inner tooth, much smaller than outer tooth.

Male.—Length, 6.0–8.0 mm. Head and thorax black; inner ventral surface of cervical sclerite sometimes with yellow spot, and sometimes small yellow spot on dorsal corner of mesepisternum; perapteron yellow. Fore- and midlegs with coxae yellow anteriorly, black posteriorly; trochanters yellow anteriorly; outside margin of femora black, inside margin of femora and tibiae and tarsi yellow; hindleg similar but black mainly at base of coxa with apical half or more yellow. Abdomen with lateral yellow spots on segments 3 or 4 to 7, sometimes small on 3; transverse yellow bands on posterior margins of segments 4 and 6.

Japan records.—Honshu: Mt. Hakkoda, Aomori Pref., 20-VII-1965, T. Naito leg. (2 ♂); Sukayu, Aomori Pref., 20-VII-1965, col. T. Naito (2 ♀, 5 ♂); Mt. Hakkoda (Towadako), Aomori Pref., 7-VIII-1988, M. Yamada (1 ♂); Mt. Iwaki, Aomori Pref., 7-VII-1995, M. Yamada (1 ♀); Sasayama, Hyogo Pref., 27-V-1954, S. Momoi (1 ♀, 3 ♂).

Remarks.—*Cephus brachycercus* occurs in Europe and has been recorded from Siberia, at least to the Irkutsk Region (Gussakovskij 1935, Verzhutskii 1966, Zhelochovtsev and Zinovjev 1996). We have not seen records from farther east, but it could occur in more eastern regions and into Japan, or it could be an introduction into Japan. The specimens agree with *C. brachycercus* specimens from Europe and key to *C. brachycercus* in existing keys (e.g., Gussakovskij 1935). It is not a species treated by Takeuchi (1938).

Many species of *Cephus* appear to be based on color differences, but coloration varies, and it is difficult to evaluate the described species. The Japanese specimens are close to *C. camtschatcalis,* but *C. camtschatcalis* lacks yellow on the mandibles and the hindleg is black with only the base of the tibia and tarsus dark brown (Enslin 1926). Also, Zhelochovtsev and Zinovjev (1996) treated *C. camtschatcalis* as a questionable synonym of *C. hyalinatus,* and these Japanese specimens are distinct from *C. hyalinatus.*

Benson (1951) mentioned that *Cephus nigrinus* Thomson, known from Europe to Siberia, is close to *C. brachycercus. Cephus nigrinus* usually has the abdomen entirely black, but Benson noted that the abdomen sometimes may have small yellow spots. He separated *C. brachycercus* by its slightly broader flagellum, with the preapical segments broader than long, its more infuscated wings, and by the sawsheath (valvula 3) not being set in a direct line with the oblong plate (valvula 2). In the Japanese specimens, the preapical antennal segments are about as broad as long, and the sawsheath is in a direct line with the oblong plate.

Because of the favorable similarity of the Japanese specimens with *C. brachycercus,* we believe it is best to refer these specimens to that species. Since we are not sure of the significance of the characters used by Benson, and since the entire genus needs revisionary study, we prefer not to describe a separate species at least until taxonomic problems within the genus are resolved.

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REVIEW OF THE NORTH AMERICAN GRAY *PYLA* GROTE (LEPIDOPTERA: PYRALIDAE: PHYCITINAE) WITH DESCRIPTION OF A NEW SPECIES FROM WESTERN UNITED STATES

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Abstract.—Eleven North American species of the "gray" section of the genus *Pyla* Grote are diagnosed by keys based on male and female genitalia. ***Pyla westerlandi* Wilterding and Balogh, new species**, is described from the Lake Tahoe region of California and central Oregon. The female of *Pyla criddlella* Dyar, previously known from only the male holotype, is described and *Phycitia bilineata* Curtis is placed as a **new synonym** of *Pyla fusca* (Haworth). The distribution, habitat, and flight period information for the gray *Pyla* species are summarized.

Key Words: life history, habitat, alvar, disjunction, genitalia, Criddle, Westerland, Aweme

Heinrich (1956) grouped nine species (four described as new) of *Pyla* Grote based on the color of the forewings in what he termed the "gray" section of the genus. Shortly thereafter, McDunnough (1958) described *Pyla gaspeensis* from the Gaspé region of Québec. Balogh and Wilterding (1998) described *Pyla arenaeola* from sandy habitats, particularly dunes, of central North America, and determined that the female of that new species was previously misassociated as the female of *Pyla aequivoca* Heinrich. In addition, *P. gaspeensis* was recognized as a synonym of *P. aequivoca.* During the course of that study, Julian Donahue (LACM) brought to our attention another new gray *Pyla* species based on material collected by the late Nils Westerland in the Lake Tahoe region of California and allowed us the opportunity to describe this distinctive moth.

Examination of nearly 1,000 specimens of North American gray *Pyla* affords us the opportunity to review the group, add considerable new distributional and habitat information, and refine the identification of the species. The female of *Pyla criddlella* Dyar (1907), known to previous authors only from the male holotype is described here for the first time. Many of the gray *Pyla* species are similar in wing color and maculation and cannot be reliably determined without examination of the genitalia. The eleven North American gray *Pyla* are readily recognized based on distinctive genital features found in both sexes as illustrated in Heinrich (1956), Balogh and Wilterding (1998), and this paper (Figs. 1–6).

All *Pyla* species, including both the "gray" and "bronzy brown" species groups of Heinrich (1956), and with the exception of the Holarctic gray species *Pyla fusca* Haworth are limited to North America. The bronzy brown *Pyla* species are restricted to montane and alpine habitats of western North America. In contrast, many gray species have western (typically north of a line from central California to Colorado) and/or transcontinental distributions in the northern states and boreal Canada (Figs. 8–10; see also *P. aequivoca,* Balogh and Wilterding 1998).

Life history information for most *Pyla* species is lacking; only the life histories of the holarctic *P. fusca* and the dune species, *P. arenaeola,* are known (Balogh and Wilterding 1998). In common with many phycitine larval strategies, the widespread *P. fusca* webs together the shoots and leaves of its hosts, primarily Ericaceae. The larvae of *P. arenaeola,* a species much more restricted in distribution occurring largely on sand dunes of the Great Lakes (Balogh and Wilterding 1998), constructs silk-lined sand tubes and feeds concealed beneath its host, bearberry, *Arctostaphylos uva-ursi* (L.) Sprengel (Ericaceae). If the life history strategy of *P. arenaeola* is representative for other *Pyla* species, larval dependence on particular substrates for shelter construction, specific ericaceous hosts, or both, might account for restricted and disjunct distribution patterns. For example, *Pyla insinuatrix* Heinrich, a species associated with fens, alvar, and coastal bogs in Nova Scotia, is distributed in a narrow band from the Atlantic coast to western Alberta (Fig. 8). *Pyla impostor* Heinrich, known from many localities in the west, has an apparently disjunct population in eastern Canada (Fig. 9). The new species described in this paper is primarily known from one locality on the northwest side of Lake Tahoe, California, and a single specimen from Crook County in central Oregon.

Specimens examined originated from the following institutions and private collections:

AMNH	American Museum of Natural History, New York, NY (F. H. Rindge).
BGS	Brian G. Scholtens, Charleston, SC.
CNC	Canadian National Collection, Ottawa, Ontario, Canada (J. F. Landry, B. Landry).
CUI	Cornell University Collection, Ithaca, NY (James Leibherr).
EGV	E. G. Voss, Mackinaw City, MI.
GJB	George J. Balogh, Portage, MI.
JAB	James A. Bess, Wanatah, IN.
JHW	John Wilterding, East Lansing, MI.
JKM	John K. Morton, Waterloo, Ontario, Canada.
KS	Ken Stead, Brantford, Ontario, Canada.
LACM	Los Angeles County Museum, Los Angeles, CA (J. P. Donahue).
LAF	Leslie A. Ferge, Middleton, WI.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA (P.D. Perkins).
MSU	Michigan State University, East Lansing, MI (F. W. Stehr).
NMNH	National Museum of Natural History, Smithsonian Institution, Washington DC (M. A. Solis).
UCB	Essig Museum, University of California, Berkeley, CA (J. A. Powell).
UM	University of Minnesota, St. Paul, MN (P. J. Clausen).
UMBS	University of Michigan Biological Station, Pellston, MI (B. G. Scholtens).
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, MI (M. F. O'Brien).
UZMH	Zoologiska Muset, Universitets Helsinki, Finland (K. Mikkola).

Keys to the Gray *Pyla*

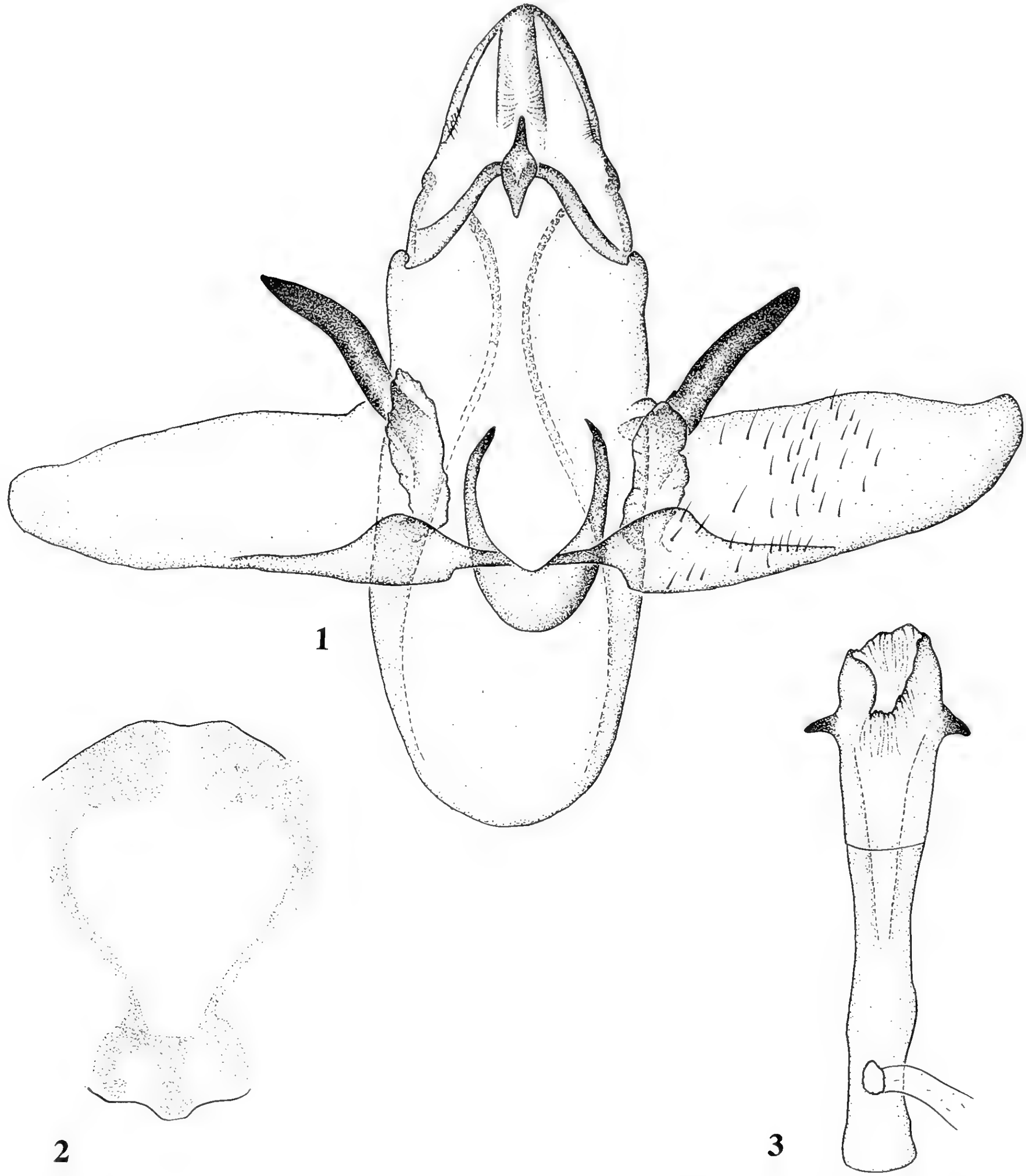
Males

In the following key the term clasper (*sensu* Heinrich) refers to a process from the mesial aspect of the valva (including valva base) and should be distinguished from the costal process, a projection from the sclerotized costal edge of the valva. All *Pyla* species included in this key have the aedeagus divided distally into two variably sclerotized lateral elements, with one or both divisions developed posteriorly into sclerotized spines or processes. In some species one division is reduced, sometimes greatly so as in *Pyla fusca* where the right division is straight, very thin, and normally appressed against the much larger left division and thus inapparent in many preparations.

1. Aedeagus with one or both lateral divisions terminating in a single, outcurved, pointed process, or the divisions symmetric and each with a single, subapical, laterally directed spine 2
– Aedeagus with each lateral division terminating as a nearly straight, or slightly incurved, blunt or pointed process, or one or both divisions with multiple distal spines (these spines may be laterally outcurved) 7
2. Aedeagus asymmetric, only one division terminating as an outcurved pointed process . . 3
– Aedeagus symmetric, each division terminating as an outcurved pointed process or each division with a single laterally directed subapical spine 4
3. Aedeagus slender, the left division outcurved and pointed, the right division very small and inapparent; vesica with a fine hairlike cornutus; valva with clasper at about ½ length, clasper knoblike and tipped with spines (Heinrich 1956, fig. 369) . . . . . *fusca* (Haworth)
– Aedeagus wider and both divisions apparent, the right division outcurved to a sharp point, the left division shorter and straight; vesica without cornutus; valva with clasper near base, clasper toothlike or triangular (Heinrich 1956, fig. 368) . . . . *criddlella Dyar*
4. Each aedeagus division terminating distally as an outcurved pointed process 5
– Each aedeagus division with a single subapical laterally directed spine 6
5. Valva with costal process at ¾ length, and clasper beyond middle of valva; juxta without spine clusters (Balogh and Wilterding 1998, figs. 1–5) . . . *arenaeola* Balogh and Wilterding
– Valva without costal process and clasper near base of valva; juxta with comb-like clusters of spines (Heinrich 1956, fig. 370) . . . . *hypochalciella* (Ragonot)
6. Tegumen with two pairs of projecting spined lobes from ventrolateral margin; valva with clasper at ½ valva length, clasper semicircular and much shorter than valva width (Heinrich 1956, fig. 367) . . . . *aenigmatica* Heinrich
– Tegumen without spined lobes; valva with clasper near base, clasper a thick, pointed curved process and longer than valva width (Figs. 1–3) . . . . *westerlandi* Wilterding and Balogh, n. sp.
7. Aedeagus with multiple distinct distal spines on one or both divisions 8
– Aedeagus with each division terminating in a blunt or pointed process and at most a single subapical spine (*P. impostor* may have a few widely scattered spinules along length of distally pointed processes) 9
8. Aedeagus divisions with one or more stout posterolaterally directed spines, more numerous on left division; juxta with paired, long, slender and pointed posterior processes; valva with clasper short and tooth-like or triangular (Heinrich 1956, fig. 366; Balogh and Wilterding 1998, figs. 6–10) . . . . *aequivoca* Heinrich
– Aedeagus divisions with multiple small apical spines; juxta without pointed elongate processes; valva with clasper an elongate spine (Heinrich 1956, fig. 371) . . . . *hanhamella* Dyar
9. Aedeagus with right division longer than left, the left with a subapical spine, each division with a helix-like twist at middle third (Heinrich 1956, figs. 362, 363) . . . *fasciolalis* (Hulst)
– Aedeagus divisions nearly equal in length and without a helix-like twist 10
10. Aedeagus divisions pointed distally; valva with clasper a long, thin, pointed process near base of valva, and valva without costal processes (Heinrich 1956, fig. 364) . . . . *impostor* Heinrich
– Aedeagus divisions blunt distally; valva with clasper a short slightly irregular ridge at ½ valva length as well as a thick and heavily spined costal process at base (Heinrich 1956, fig. 365) . . . . *insinuatrix* Heinrich

Females

1. Ostium bursae with dense ventrolateral sclerotization, sclerotized projections, or scobinate lobes or plates 2
– Ostium bursae membranous, or only lightly sclerotized with fine granulations or folds . . 9
2. Corpus bursae with extensive convolute sclerotized folds on posterior half (Heinrich 1956, fig. 850) . . . . *impostor* Heinrich
– Corpus bursae membranous or with at most weakly developed small patches of sclerotization 3
3. Ductus bursae sclerotized posteriorly and with lateral margins subparallel, the sclerotization extending onto ostium bursae and var-



Figs. 1–3. *Pyla westerlandi,* male genitalia. 1, Genital capsule, valves spread, aedeagus removed, ventral view. 2, Eighth sternite, ventral view, without scale tufts. 3, Aedeagus, ventral view.

iably developed into a ventrolateral sclerotized rim 4

– Ductus bursae without dense sclerotization, outer margins bulge laterally, or if lateral margins subparallel, ductus bursae semimembranous; ostium bursae with paired ventrolateral sclerotized plates or scobinate lobes 6

4. Ostium bursae ventrolateral sclerotization a sinuate, liplike band; ductus seminalis from right-sided lobe of the corpus bursae (Heinrich 1956, fig. 860) . . . . *hanhamella* Dyar

– Ostium bursae otherwise modified; ductus seminalis from the dorsal aspect of the corpus bursae 5

5. Ostium bursae sclerotization paired convolute sclerotized lobes with deep central notch (Heinrich 1956, fig. 853) . . . *aenigmatica* Heinrich

– Ostium bursae sclerotization funnel shaped and without deep central notch (Heinrich 1956, fig. 854) . . . . . *hypochalciella* (*Ragonot*)

6. Ostium bursae with paired, pad-like, rounded, scobinate ventrolateral lobes; ductus bursae strongly dorsoventrally flattened, lateral margins subparallel and distinctly narrower than the width of posterior aspect of corpus bursae (Heinrich 1956, fig. 856) . . *insinuatrix* Heinrich

– Ostium bursae with paired, densely sclerotized, ventrolateral convolute and/or scobinate plates; ductus bursae not stongly dorsoventrally flattened, lateral margins bulging and subequal in width to posterior aspect of corpus bursae (when the bursae is well inflated) 7

7. Ostium bursae with elongate, triangular, sclerotized, ventrolateral plates (Heinrich 1956, fig. 855 [as *aequivoca*]; Balogh and Wilterding 1998, figs. 11–13) . . . . *arenaeola* Balogh and Wilterding

– Ostium bursae with convolute, sclerotized, ventrolateral plates that are not distinctly triangular in shape 8

8. Ostium bursae paired sclerotized plates as long or longer than wide; ostium bursae a large rectangular chamber; ductus bursae membranous, with lateral walls bulging somewhat asymmetrically to the left (Fig. 4) . . . . *westerlandi* Wilterding and Balogh, n. sp.

– Ostium bursae paired sclerotized plates shorter than wide; ostium bursae not rectangular in shape; ductus bursae partially sclerotized laterally with walls symmetrically bulging laterally (Balogh and Wilterding 1998, figs. 14–16) . . . . *aequivoca* Heinrich

9. Ostium bursae membranous and weakly constricted at junction with ductus bursae; ductus and corpus bursae with extensively developed, convolute, sclerotized bands that extend onto anterior half of corpus bursae (Heinrich 1956, fig. 849) . . . . *fasciolalis* (Hulst)

– Ostium bursae with fine granulations or partially sclerotized folds and obviously constricted at junction with ductus bursae; ductus and corpus bursae sclerotization smooth or convoluted but not extending onto anterior half of corpus bursa 10

10. Ductus and corpus bursae elongate with smooth elongate bands of sclerotization and lacking diverticula (other than the lobe at insertion of ductus seminalis) (Heinrich 1956, fig. 852) . . . . *fusca* (Haworth)

– Ductus and corpus bursae globular in shape; an oblique, convolute band of sclerotization near ductus-corpus bursae junction and multiple adjacent diverticula (in addition to the lobe at insertion of ductus seminalis) (Figs. 5, 6) . . . . *criddlella* Dyar

Pyla fasciolalis (Hulst)
(Fig. 7; Heinrich 1956, figs. 362, 363, 849)

Pinipestis fasciolalis Hulst 1886: 162. Holotype ♂, "Spencers Bridge" (Rindge 1955) [= Spence's Bridge, NW of Nicola (J. D. Lafontaine, personal communication 1999)], British Columbia, Canada (AMNH). [In the original description the type locality is in error as Nevada, see Heinrich (1956) and Rindge (1955).] [Type examined.]

Pyla fasciolalis is known from scattered localities in western North America (Fig. 7), with most localities represented by single specimens. Recorded elevations in the northern portion of the distribution range from 2,100 feet (3 mi W Nelson, British Columbia) to 5,500 feet (Manning Park, Valley View, British Columbia) and the moth has been collected as high as 10,150 feet farther south (Crooked Creek Lab, Mono Co., California). In northeastern Utah (Sheep Creek and Highway 44) a small series was collected in mixed sage-juniper and riparian habitat (GJB). Flight dates range from 7 June to 13 August. The life history is unknown.

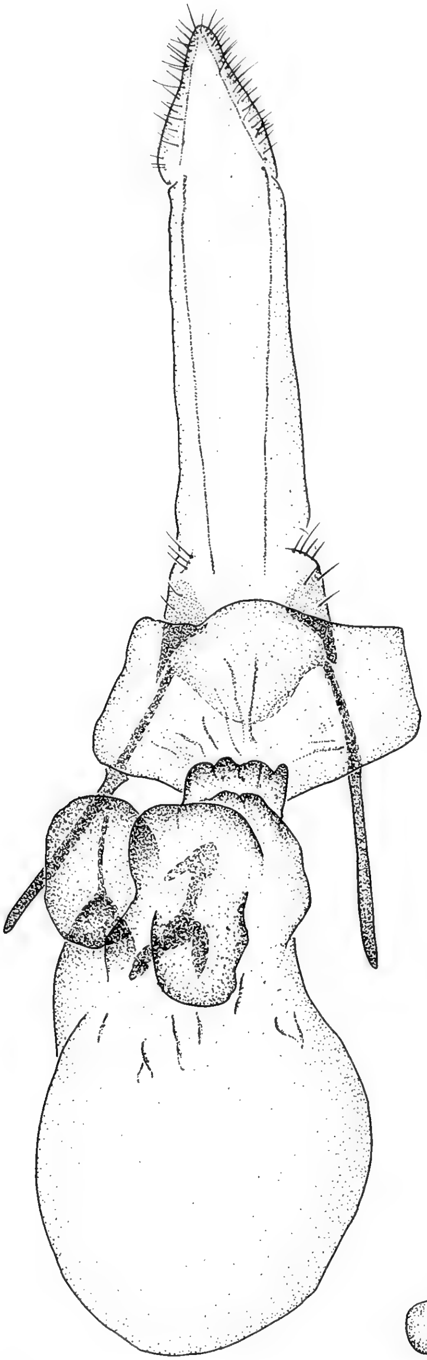
Heinrich (1956) noted variation in genital details perhaps worthy of additional study as additonal material becomes available. However, the twisted asymmetric lateral processes of the male aedeagus (Heinrich 1956, fig. 362a) and configuration of the female corpus bursae (Heinrich 1956, fig. 849) distinguish *P. fasciolalis* from all other *Pyla* species.

Material examined: 13 ♂, 7 ♀ [AMNH, CNC, GJB, LACM, NMNH, UCB, UM].

Pyla impostor Heinrich
(Fig. 9; Heinrich 1956, figs. 364, 850)

Pyla impostor Heinrich 1956: 143. Holotype ♂, Slate Peak, 6,500–7,000 ft, Whatcom County, Washington, United States (NMNH). [Type examined.]

Pyla impostor is a widely distributed western species with most documented lo-



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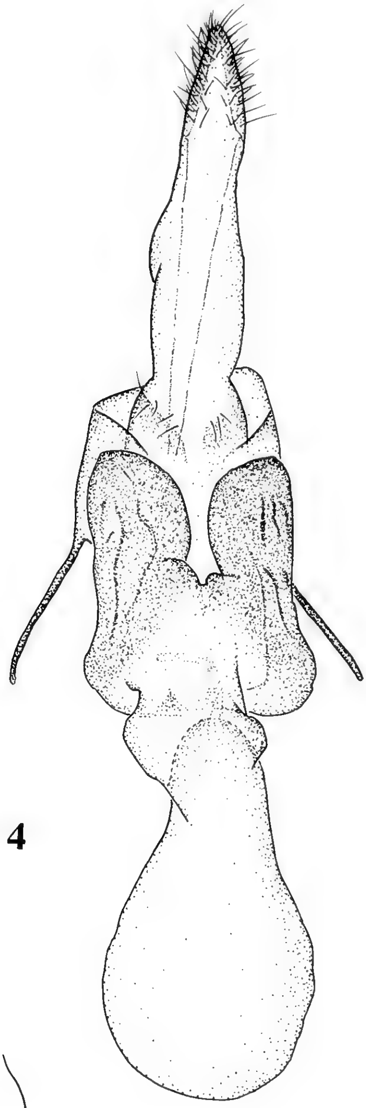

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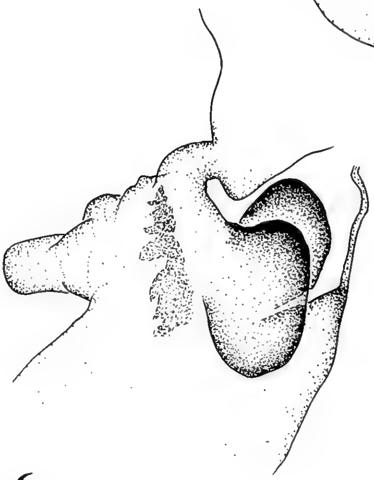

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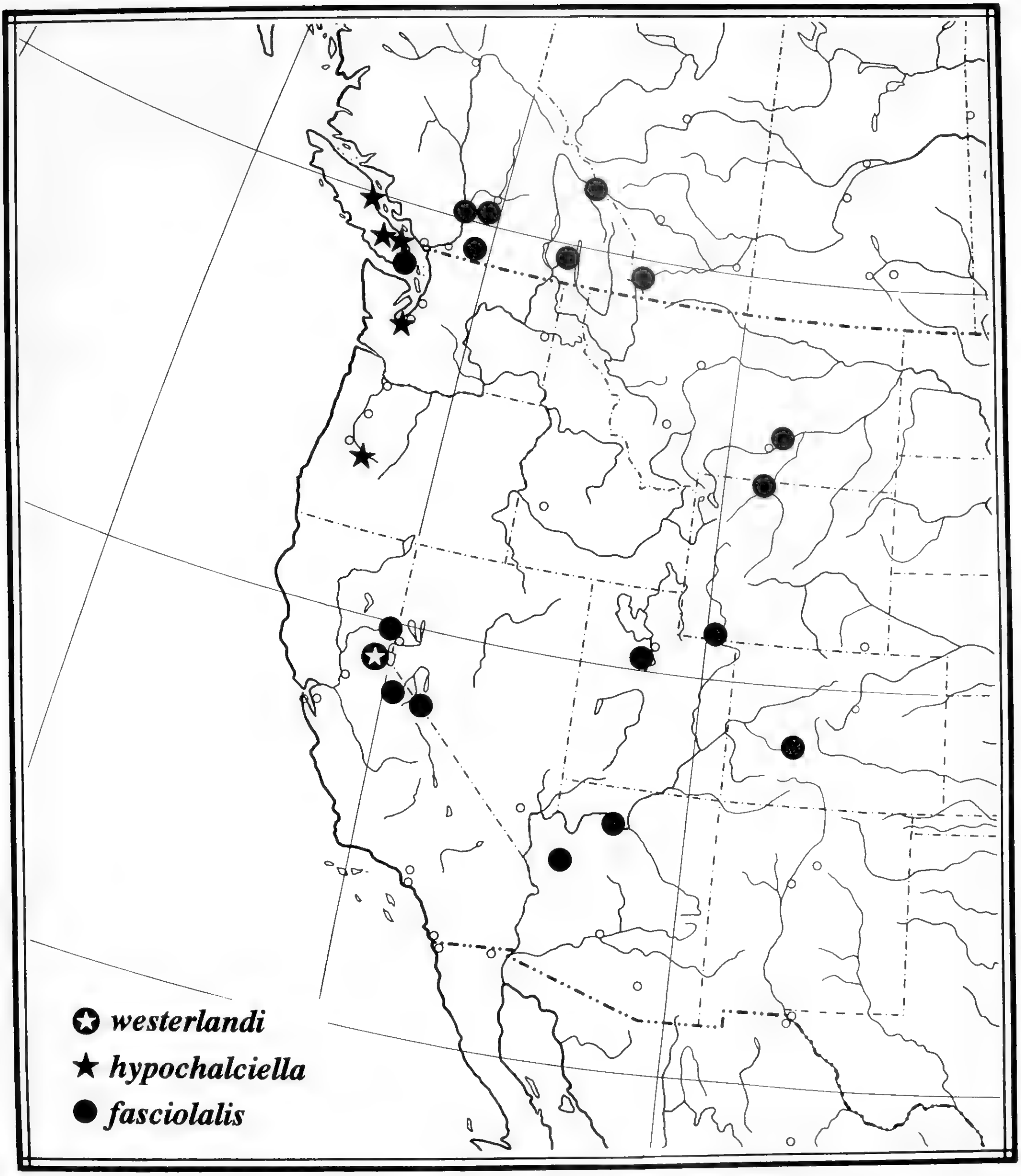


Fig. 7. Known distribution of *Pyla westerlandi, P. hypochalciella,* and *P. fasciolalis* in western North America.

←

Figs. 4–6. *Pyla westerlandi* and *P. criddlella,* female genitalia. 4, *P. westerlandi,* genital capsule, ventral view. 5–6, *P. criddlella.* 5, Genital capsule, ventral view. 6, Right lateral aspect of ductus bursae and posterior portion of corpus bursae.

calities in the Rocky Mountains and northern Cascades (Fig. 9). Additional material was also examined from the southern Cascades, central Sierra Nevada region, and more isolated mountain ranges including the Wallowa Mountains of northeastern Oregon, the Snake Range of eastern Nevada, and the San Francisco Mountains of northern Arizona. Seemingly disjunct localities include Chilkat Pass, British Columbia-Yukon Territory border (3,200 feet) and three localities in the eastern St. Lawrence region of Canada (Knob Lake and Laurentides Park, Quebec; Cartwright, Labrador). In the northern Rockies and Cascades recorded elevations range from 4,000 to 9,000 feet; recorded elevations in the southern Rockies, central Sierra Nevada, Snake Range, and San Francisco Mountains from 6,250 to 10,400 feet. Flight dates range from 1 July to 27 August. The life history is unknown.

The eastern specimens (5 males) are indistinguishable from western populations based on genitalia. Similar eastern disjunct distributions of otherwise western montane moths and plants have been documented where the eastern portion of the range includes the Great Lakes, eastern St. Lawrence, and Atlantic Coast or some combination of these regions. Examples in the Noctuidae include *Euxoa shasta* Lafontaine, *E. tristicula* (Morrison), *E. quebecensis* (Smith), and *E. macleani* McDunnough (Lafontaine 1982, 1987) and in the Geometridae *Eupithecia sharronata* Bolte (Bolte 1990). Marquis and Voss (1981) discuss this distribution pattern in detail for plants with particular attention to the Great Lakes region. Review of the distribution maps recently published for North American pteridophytes (Flora of North America Editorial Committee 1993) provides additional examples. However, true disjuctions are difficult to distinguish from artifactual distribution gaps in poorly sampled taxa such as in the phycitines.

Material examined: 75 ♂, 41 ♀ [AMNH, CNC, GJB, LACM, MSU, NMNH, UCB, UZMH].

Pyla aequivoca Heinrich
(Balogh and Wilterding 1998, figs. 6–10, 14–16, 18, 23–28; Heinrich 1956, fig. 366)

Pyla aequivoca Heinrich 1956: 143. Holotype ♂, Banff, Alberta, Canada (CNC). [Type examined.]

Pyla gaspeensis McDunnough 1958: 5. Holotype ♂, Mile 49, Cascapedia Road, Gaspé, Québec, Canada (CNC). Allotype ♀, Cascapedia Road, near Mt. Albert, Gaspé, Québec, Canada (NMNH). [Types examined.]

Pyla aequivoca, a boreal and western montane species, was recently redescribed with notes on its distribution and habitiat (Balogh and Wilterding 1998). The life history is unknown.

Material examined: 35 ♂ and 35 ♀ [AMNH, CNC, EGV, GJB, LACM, MSU, NMNH, UZMH].

Pyla insinuatrix Heinrich
(Fig. 8; Heinrich 1956, figs. 365, 856)

Pyla insinuatrix Heinrich 1956: 144. Holotype ♂, Aweme, Manitoba, Canada (CNC). [Type not examined.]

Pyla insinuatrix is distributed along a narrow region extending across southern Canada and the northern United States from Nova Scotia to western Alberta (Fig. 8). This moth is associated with wet calcareous habitats in the Great Lakes region including northern fens, interdunal wetlands, alvar, and swampy stream sides and it is also known from coastal bogs in Nova Scotia (D. C. Ferguson, personal communication 1995). On Manitoulin Island and the nearby smaller islands of Georgian Bay, Ontario, it has been recorded from a dozen localities and often associated with alvar (John K. Morton, personal communication 1999). In northern Michigan *P. insinuatrix* is common on Drummond Island at the southern edge of the Maxton Plain where moist alvar

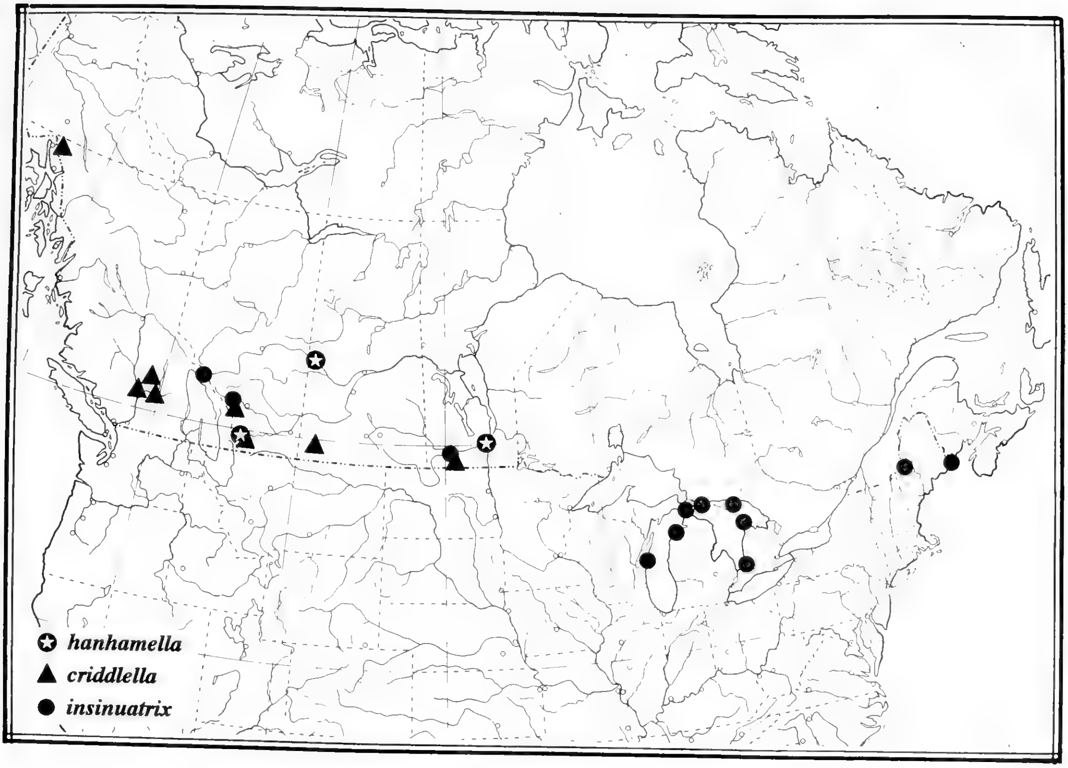


Fig. 8. Known distribution of *Pyla hanhamella, P. criddlella,* and *P. insinuatrix* in North America.

grades into a large sedgy wetland. Flight dates range from 11 June to 24 August with most records during July and August. The life history is unknown.

Material examined: 55 ♂, 9 ♀ [CNC, GJB, JKM, KS, LAF, MSU, NMNH, UZMH].

Pyla aenigmatica Heinrich
(Fig. 9; Heinrich 1956, figs. 367, 853)

Pyla aenigmatica Heinrich 1956: 144. Holotype ♂, Wellington, British Columbia, Canada (NMNH). [Type not examined.]

Pyla aenigmatica is transcontinentally distributed but infrequently encountered, recorded from scattered localities extending from the Gaspé region of Québec west to Vancouver Island, British Columbia and as far south as Sevier Co., Utah (Fish Lake) (Fig. 9). This moth is unevenly distributed along the major mountain ranges of the west but is not associated with high montane habitat. In the Great Lakes region, specimens of *P. aenigmatica* have been collected in sandy and rocky habitats but rarely on moving dunes. Flight dates range from 4 June to 3 September. The life history is unknown.

Material examined: 25 ♂, 14 ♀ [AMNH, CNC, GJB, JKM, MSU, NMNH, UCB, UM].

Pyla criddlella Dyar
(Figs. 5, 6, 8, 11, 12; Heinrich 1956, fig. 368)

Pyla criddlella Dyar 1907: 110. Holotype ♂, Aweme, Manitoba, Canada (NMNH). [Type examined.]

Diagnosis.—*Pyla criddlella* is the smallest of the gray *Pyla* with brownish gray wings and indistinct maculation (Figs. 11, 12). The genitalia are diagnostic in both

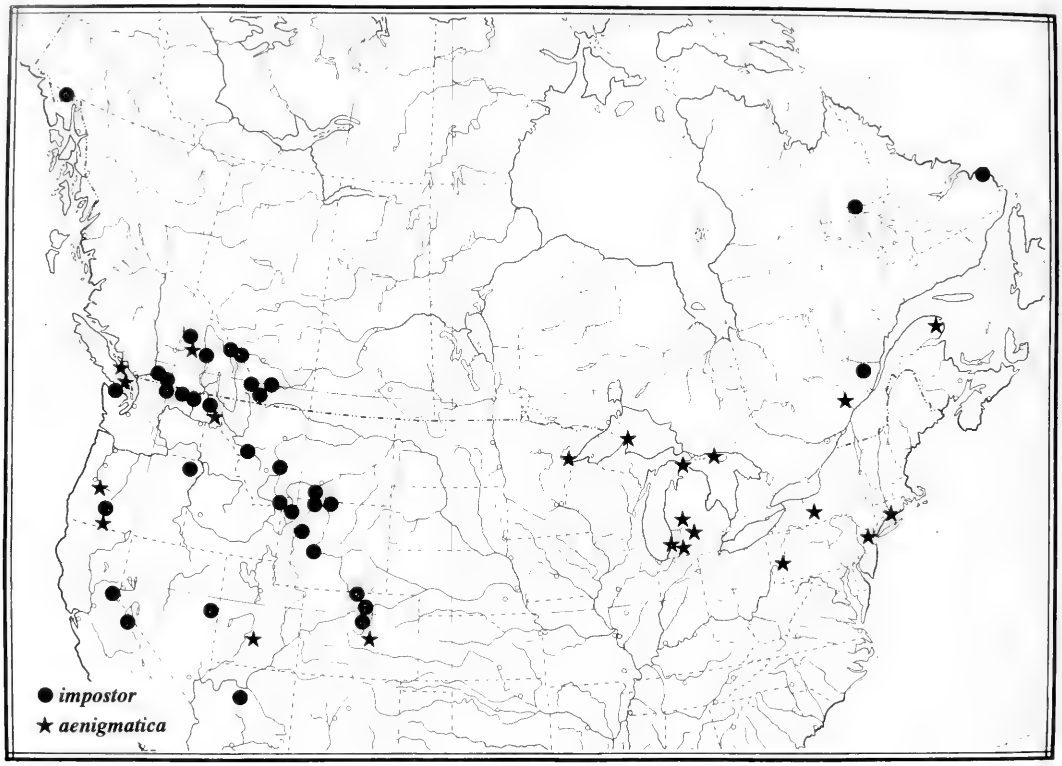


Fig. 9. Known distribution of *Pyla impostor* and *P. aenigmatica* in North America.

sexes. The male aedeagus is asymmetric with the lateral divisions separated by a membranous gap, and the right division developed distally into a posterolaterally directed pointed spine (Heinrich 1956, fig. 368a). The female ostium bursae is semimembranous without heavily sclerotized plates or processes; the posterior portion of the corpus bursae has a short convolute band of sclerotization with three adjacent diverticula (Figs. 5, 6).

Redescription.—*Alar expanse:* 18.1 to 22.4 mm (mean = 20.8 mm, n = 7) *Vestiture:* A mixture of semilustrous light and dark brownish gray scales, many scales white tipped, darker and browner than most other gray *Pyla* species. *Head:* Frons convex, scaled brownish gray; male vertex shallowly concave with appressed central lustrous brownish scaling, female vertex flat with loose central pale-tipped scaling, ocelli and chaetosemata well developed; labial palpus thick, porrect, length 2½–3× width of eye, 2nd segment longest and broadest, scaled with brownish gray and pale-tipped scales, base and mesial aspect paler; maxillary palpus with tufts of narrow scales extending to ½ length labial palpus; tongue well developed, covered proximally with brownish gray scales; antenna laminate, basal segments of male flagellum modified forming a mesial sinus, each modified segment with a distal spine, spines progressively larger distally, sinus bordered medially and laterally by rows of gray scales, inner row of scales forming medial border of sinus modified, thick, dark, each with curved central spine-like tooth, base of female flagellum unmodified, unmodified segments of flagellum in both sexes scaled pale brown, scape nearly uniform brownish gray. *Thorax:* Dorsum, tegula, and collar and ventral aspect of thorax gray or brownish gray, scales sometimes faintly pale-tipped; legs similar in color, mesial aspect paler, tarsal segments white-tipped distally, protibia with spine-tipped epiphysis from middle extending just distal to first tarsal joint, mesotibia with one and metatibia with two pair of spurs. *Wings* (Figs. 11–12): Forewing dark semilustrous brownish gray sprinkled with white-tipped scales; markings faintly contrasting, antemedial and postmedial lines indicated by slightly greater concentration of white-tipped scales, bordered with slightly darker shade, antemedial oblique, postmedial indented opposite cell and in lower third, discal mark and terminal line absent; fringe paler brownish gray white-tipped scales; underside brownish gray, paler along inner margin, vague indication of postmedial line, fringe nearly unicolorous, paler at base. Hindwing brownish gray, lighter than forewing, veins slightly darker; fringe paler, a thin pale line at base; underside concolorous with upperside of hindwing and underside of forewing, fringe paler. *Abdomen:* Brownish gray, slightly paler than thorax.

Male genitalia (Heinrich 1956: fig. 368): Uncus subtriangular and hood-like; gnathos with a stout central hook; valva narrow, tapered in distal third, slightly greater degree of sclerotization along proximal ¾ of costa and proximal ½ of sacculus; clasper (*sensu* Heinrich) at costal aspect of valva base, a slightly irregular sclerotized ridge developed into a short medial triangular or tooth-like process; tegumen unmodified; juxta developed into a rounded pocket anteriorly, weakly sclerotized lateral to the aedeagus, without posterior processes; aedeagus (Heinrich 1956, fig. 368a) divided distally, divisions asymmetric, sclerotized, the right longer, thicker, semi-cylindrical, developed into a lateral sclerotized spine distally, vesica with fine scobinate patch, cornuti absent; anellar membrane with small pouches dorsal to basal process of valva; eighth abdominal sternite with a pair of hair pencils.

Female genitalia (Figs. 5–6): Ostium bursae finely scobinate, semimembranous, funnel-shaped, lamella antevaginalis with weakly sclerotized folds radiating to junction of ostium bursae and ductus bursae; junction of ostium bursae and ductus bursae weakly convoluted, membranous and slightly fleshy; ductus bursae short, curved, arising ventrally from ostium bursae; corpus bursae largely membranous, posterior half coarsely wrinkled with an oblique convoluted band of sclerotization, three small membranous diverticula from posterior half of corpus bursae, two dorsal, one ventral; ductus seminalis arising from a sclerotized dorsal outpouching on the left; ovipositor telescoped, less than half length of genital capsule, ovipositor lobes slightly concave laterally.

Holotype.—♂ "Criddle, Aweme, Man., 10.VI.04"; "Type"; "Genitalia Slide, By 101,103, USNM"[green label]; "Type, No. 10344, U.S.N.M." [red label]; "[male symbol] genitalia on, slide 30 Jan 1942, C.H. 2780" (NMNH).

Material examined.—(6 ♂, 12 ♀) CANADA. Alberta: 1 ♀, 28 Jun 1923, Waterton Lakes (CNC); 1 ♂, 1 Jul 1923, Waterton Lakes (CNC); 1 ♂, 1 ♀, 2 Jul 1922, Banff (CNC). British Columbia: 1 ♀, 11 Jul 1937, Jesmond (CNC); 2 ♀, 11 Jul 1937, Jesmond, 1,500′ (CNC); 1 ♀, 9 Jul 1923, Jesmond, 3,500′ (CNC); 1 ♀, 13 Jul 1937, Jesmond (CNC); 1 ♂, 22 July 1937, Jesmond (CNC); 1 ♀, 22 Jul 1937, Jesmond, 7,500′ (CNC); 1 ♂, 23 Jun 1938, Canim Lake (CNC); 1 ♀, 28 Jun 1937, Kamloops (CNC); 1 ♂, 30 Jun 1955, Atlin, 2,200′ (CNC). Manitoba: 1 ♂, 1 ♀, 16 Jun 1904, Aweme (CNC); 1 ♀, 10 Jun 1926, Aweme (CNC). Saskatchewan: 1 ♀, 3 June 1926, Cypress Hills, nr Maple Creek (CNC).

Discussion.—*Pyla criddlella* was previously described from a single male (Dyar 1907, Heinrich 1956). The female is described here for the first time. Unlike other gray *Pyla, P. criddlella, P. hanhamella* Dyar, and *P. hypochalciella* (Ragonot) are brown or brownish gray moths but not distinctly lustrous bronzy-brown. *Pyla criddlella* is the smallest of the gray *Pyla* and its distribution is poorly known (Fig. 8).

The documented distribution includes southwestern Manitoba (Aweme), southern Saskatchewan (Cypress Hills), southwestern Alberta (Waterton Lakes, Banff) and south central British Columbia (Jesmond, Kamloops, Canim Lake); specimens examined from these localities were collected between 1904 and 1938. A single male was collected at Atlin in northwestern British Columbia in 1955. Flight dates range from 3 June to 22 July and the life history and habits are unknown. Perhaps the small number of records and lack of recent collections reflects narrow habitat requirements.

History and etymology.—*Pyla criddlella* is named for the Canadian entomologist Norman Criddle (1875–1933), a well known illustrator and agricultural entomologist who avidly studied and collected insects in southwestern Manitoba. The Criddle homestead and farm, southeast of Brandon, Manitoba, is in a region of mixed sandy prairie, forest (primarily white spruce, *Picea glauca* (Moench) A. Voss; and poplar, *Populus tremuloides* Michaux), and wetland supporting tamarack (*Larix laricina* (DuRoi) K. Koch) and black spruce (*Picea mariana* (Miller) BSP.). A fossil sand dune system, the Carberry Desert or Bald Head Hills, is evident as actively moving open sand deposits to the east of the homestead. Norman Criddle frequently made day collecting trips into these sand hills. Despite the local diversity of habitats, all Criddle material is labeled Aweme, a name given to his entomological lab and the local post office (Criddle 1973). Bird (1927) and Criddle (1915) described the habitats in the vicinity of Aweme.

Norman's father Percy Criddle (1844–1918) and other members of the family had diverse interests in natural history. Percy was unquestionably proud of Norman's accomplishments and his ego bolstered, if he was not somewhat amused, as insects took on the Criddle namesake:

> "I expect to find myself elected corresponding member of at least six learned societies in Ontario and elsewhere immediately, on account of my butterfly collection—buffalo bones—and chunks of old stones. While my new friends anticipate a brilliant future and immortality owing to my possible discovery of some new insect or other in this unexplored district which will be of course called 'Criddle-de-diddle-ensis' or some other fancy family name." [Entry from Percy Criddle's diary, one year after immigrating to Manitoba from England, following his visit with Ernest Thompson Seton and 'Mr. Christie' in 1883 (Criddle 1973: 94).]

Pyla fusca (Haworth)
(Fig. 10; Heinrich 1956, figs. 369, 852)

Phycis fusca Haworth 1811: 493. England. [Location of type unknown.]

Phycis spadicella Zincken 1818: 168. ♂ and ♀ syntypes indicated in original description, Augsburg, Germany. [Types not examined.]

Phycis janthinella carbonariella Duponchel 1836: 292; plate 281, fig. 2. Syntypes not itemized in original description, Domo d'Ossola, Italy. [Types not examined.]

Phycis posticella Zetterstedt [1839]: 996. Syntypes 1 ♂, 1 ♀, Lapland (Riksmuseum, Stockholm, Sweden). [*Physis posticella* Zetterstedt is treated as a synonym of *Salebria fusca* Haworth by Benander (1940).] [Types not examined.]

Phycis annulatella Zetterstedt [1839]: 997. Syntypes 1 ♂, 2 ♀, Lapland (Riksmuseum, Stockholm, Sweden). [*Phycis annulatella* Zetterstedt is treated as a synonym of *Salebria fusca* (Haworth) by Benander (1940), and is noted to be a junior synonym of *Pyla fusca* (Haworth) by Speidel (1996). Speidel (1996) further notes that *P. annulatella* sensu Ragonot is the misidentified type species of *Polopeustis* Ragonot.] [Types not examined.]

Phycitia bilineata Curtis 1850: 114. 1 ♂ is indicated in the original description, Norfolk, England (syntypes in Melbourne Museum, Australia). [This was an unpublished **new synonymy**, M. Schaffer per-

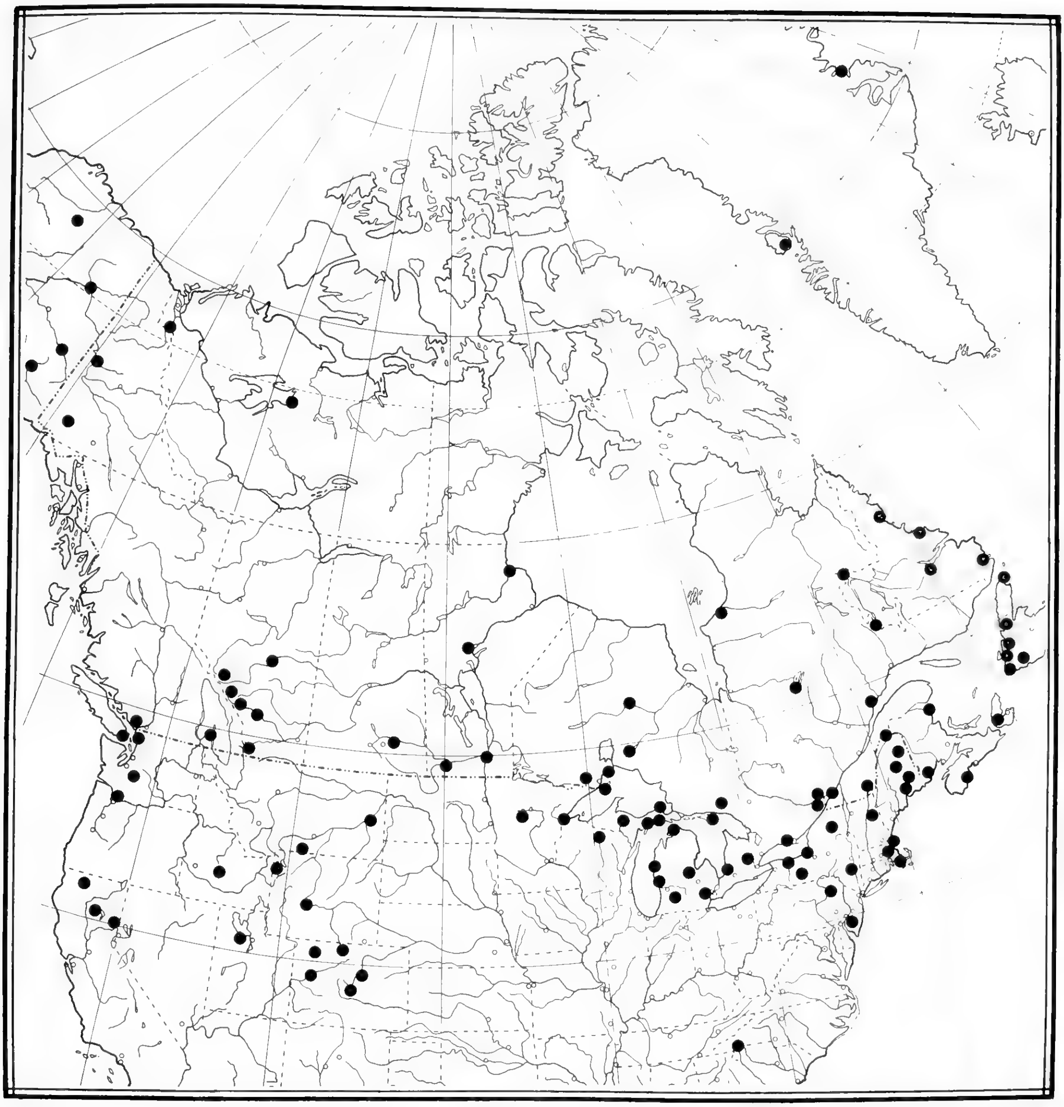


Fig. 10. Known distribution of *Pyla fusca* in North America, including Greenland.

sonal communication 1999.] [Types not examined.]

Nephopteryx moestella Walker 1863: 53. Extant syntypes include 1 ♀ from Nova Scotia, 4 ♀ from St. Martin's Falls, Ontario, and possibly 1 ♀ with no data that carries Walker's name label; no lectotype designated (BMNH). [Note: Walker's description clearly indicates that both sexes were represented in the type series and he itemized three specimens from the United States, five from St. Martin's Falls, and one from Nova Scotia.] [Types not examined.]

Paedisca procellariana Walker 1863: 379. Holotype ♀, Arctic America (BMNH). [Type not examined.]

Eudorea "?" *frigidella* Packard 1867: 53. Syntype ♂ [abdomen missing], Caribou Island [= Great Caribou Island], Labrador, Canada (MCZ). [Note: Packard did not indicate the number or sex of the specimens in his type series. The date of publication follows Miller and Hodges (1990). The MCZ syntype is labeled "Labrador" and likely is one of a series of specimens from which Packard described *frigidella.* Subsequently Packard (1873) recognized that his *frigidella* was a synonym of *Pempelia fusca* (Haworth) and the syntype is so labeled by Packard. This specimen also bears a label "*Eudorea borealis* n. sp.," a combination not published by Packard but likely a mislabeling as the name *Pyrausta borealis* Packard was published on the same page as *Eudorea ? frigidella. Pyrausta borealis* Packard is now treated as a subspecies of *Pyrausta subsequalis* (Gn.) (Hodges et al. 1983)]. [Type examined.]

Pinipestis cacabella Hulst 1887: 133. Holotype ♂, New York, United States (AMNH). [Note: New York is given as the type locality in the original description but the type lacks a locality label as noted by Heinrich (1956) and Rindge (1955).] [Type examined.]

Salebria triplagiella Dyar 1904: 109. Holotype ♂, Winnipeg, Manitoba, Canada (NMNH). [Type examined.]

Pyla fusca is the most commonly encountered and widely distributed *Pyla* in North America and ranges from the arctic south to New Jersey, North Carolina, and the Great Lakes region in the east and to Colorado and northern California in the west (Fig. 10). As the only holarctic *Pyla,* it is also widespread in northern and central Europe and Asia, and recorded from Greenland and Iceland (Speidel 1996, Sinev 1997, Wolff 1971). Based on European records the larvae primarily feed on the shoots and leaves of Ericaceae (Goater 1986, Palm 1986). Darlington (1952) cites a rearing from "blueberry" at Anglesea, New Jersey. Flight dates range from 25 May to 23 September.

Although *P. fusca* deviates from other *Pyla* species based on the presence of a cornutus on the male vesica, the aedeagus is divided as in other *Pyla* species but with one division very fine and closely appressed to the opposite, distally curved, and more heavily sclerotized division. The presence of two divisions is not apparent in published figures of Heinrich (1956, fig. 369a).

We are indebted to Michael Shaffer (The Natural History Museum, London) for permitting us to publish the above synonomy for *Pyla fusca.*

Material examined: 107 ♂, and 128 ♀ [AMNH, CNC, CUI, GJB, JKM, KS, LACM, MCZ, MSU, NMNH, UM, UMMZ, UZMH].

Pyla hypochalciella (Ragonot)
(Fig. 7; Heinrich 1956, figs. 370, 854)

Nephopteryx ovalis hypochalciella Ragonot 1887: 7. Type a single specimen of indeterminate sex and in poor condition [E. Cudel, personal communication 1998], Washington Territory (Paris Museum). [Type not examined.]

Pyla blackmorella Dyar 1921: 68. Holotype ♂, Mt. Tzouhalem, Duncan, British Columbia, Canada (NMNH). [Type examined.]

Pyla hypochalciella is an infrequently collected species from the Pacific Northwest (Fig. 7), most specimens are known from central and southern Vancouver Island, British Columbia, with single specimens examined from Tenino, Washington and Baker, Oregon, all collected between 1913 and 1947. Flight dates range from 1 June to 4 July. Life history and habits are unknown.

Specimens of *P. hypochalciella* are found mixed in collections with a superficially similar phycitine, a brown species of *Catastia* Hübner that occurs to the east in the Cascade Mountains. *Pyla* and *Catastia* are readily distinguished by genitalia in both sexes (Heinrich 1956). Males can also be separated by examination of the modified basal segments of the antenna, which are developed into a sinus in both genera.

In *P. hypochalciella* the spines within the sinus are short and exceeded and partially covered by a tuft of long curved scales along the mesial aspect of the sinus; in the *Catastia* species the spines are long, the distal spines exceeding the shorter mesial scale tuft. The row of scales along the inner border of the sinus are modified distally into spine-like processes in *P. hypochalciella* (as in other gray *Pyla*) whereas these scales are rounded distally with multiple fine teeth in the *Catastia* species.

Material examined: 7 ♂ and 5 ♀ [CNC, NMNH].

Pyla hanhamella Dyar
(Fig. 8; Heinrich 1956, figs. 371, 860)

Pyla hanhamella Dyar 1904: 109. Holotype ♂, Winnipeg, Manitoba, Canada (NMNH). [Type examined.]

Pyla hanhamella is recorded from relatively few localities in west central North America (Fig. 8) including central and southern Manitoba (Aweme; 2 miles west of Stockton; Onah; Winnipeg; "C[entral] Manitoba"), western North Dakota (Columnar Juniper Area, Slope county; not mapped), western Saskatchewan (Harlan), and southwestern Alberta (Hillcrest; Waterton Lakes). A single male was flushed from short-grass prairie in the badlands of Slope Co., North Dakota near midday, June 12, 1991 (GJB) (see photograph of habitat in McCabe and Post 1977, fig. 24). Flight dates range from 20 May to 25 July. The life history is unknown.

Material examined: 13 ♂, 12 ♀ [AMNH, CNC, GJB, NMNH].

Pyla arenaeola Balogh and Wilterding
(Balogh and Wilterding 1998, figs. 1–5, 11–13, 17, 19–22)

Pyla arenaeola Balogh and Wilterding 1998: 705. Holotype ♂, Saugatuck Dunes State Park, Allegan County, Michigan, USA (42.39′18″N, 86.12′07″W) (NMNH).

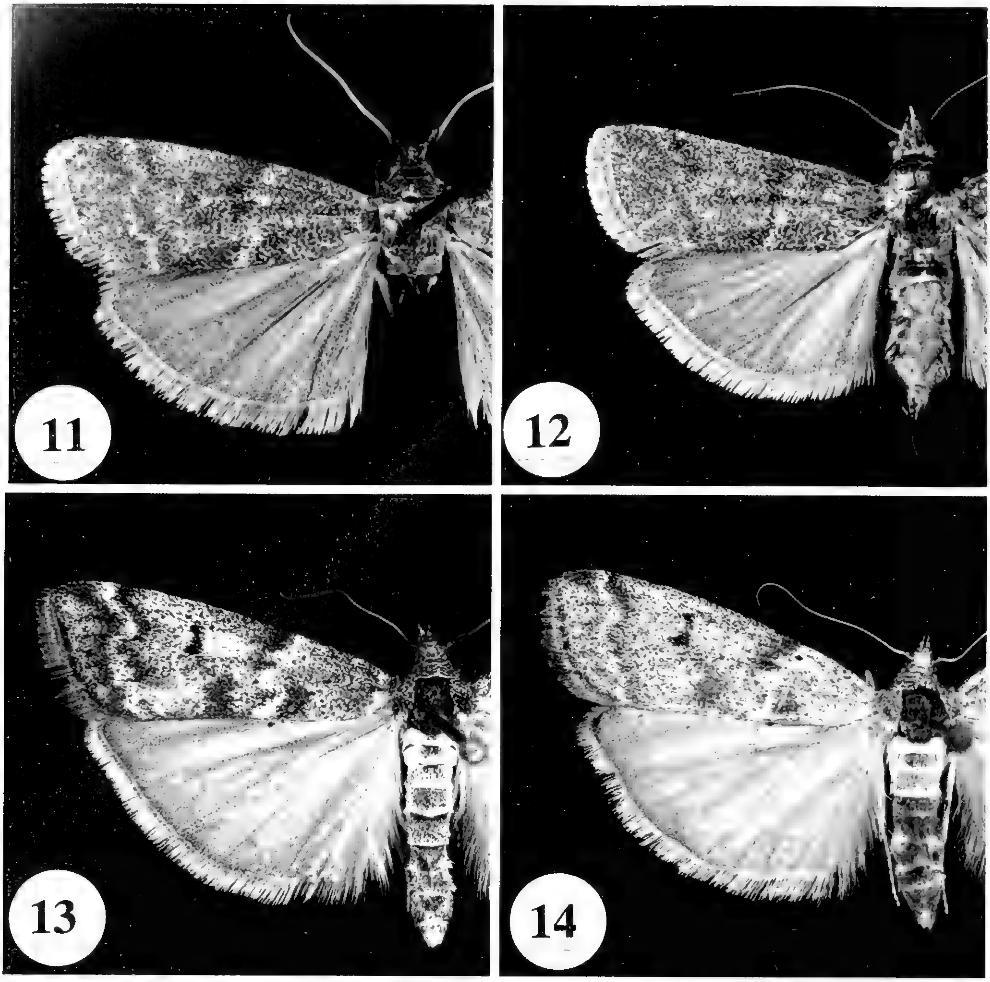
Pyla arenaeola is known only from the dunes of the Great Lakes and southwestern Manitoba (Balogh and Wilterding 1998, fig. 17); the larvae live hidden in sand tubes and feed on Bearberry (*Arctostaphylos uva-ursi*). Details of the life history, habits, and biogeography of *P. arenaeola* can be found in Balogh and Wilterding (1998). Additional specimens collected on the southern shore of Lake Huron were examined since publication of the original description (CANADA: Ontario, Lambton County, Port Franks, 1 ♂, 30 Jul 1997 and 1 ♀, 7 Aug 1998 [KS]).

Material examined: 162 ♂, 95 ♀ [BGS, CNC, GJB, JAB, JHW, JKM, KS, LAF, MSU, NMNH, UMMZ].

***Pyla westerlandi* Wilterding and Balogh, new species**
(Figs. 1–4, 7, 13, 14)

Diagnosis.—This species is on average the largest gray *Pyla* species, but like other species of the group, is best recognized by features of the male and female genitalia. Males have an unusually long and stout clasper (*sensu* Heinrich) near the base of the valva and the aedeagus has symmetric laterally directed thorn like spines distally (Fig. 3). Females have an unusually large rectangular ostium bursae with a pair of rounded heavily sclerotized ventrolateral plates (Fig. 4).

Description.—*Alar expanse:* 29.7 to 36.2 mm (mean = 33.2 mm, n = 22). *Vestiture:* A mixture of gray, pale gray, whitish, and pale tipped gray scales. *Head:* Frons convex, a broad tuft of pale-tipped gray scales superiorly, paler scaling ventrally; male vertex concave with appressed central scaling and an anterior row of thicker and narrower brownish scales, female vertex nearly flat with loose central scaling, in both sexes most scales gray, often pale tipped, a tuft of elongate pale-tipped gray scales posteriorly; ocelli and chaetosemata well developed; labial palpus ascending to level of vertex, 2nd segment longest and broadest and in male with medial groove for maxillary palpi, 3rd segment thin, ⅓ length of 2nd, scaled with gray and whitish



Figs. 11–14. *Pyla criddlella* and *P. westerlandi* adults. 11–12, *P. criddlella.* 11, male, Waterton Lakes, Alberta. 12, female, Cypress Hills, Saskatchewan. 13–14, *P. westerlandi.* 13, Holotype male, Ward Creek, 2 mi S. Tahoe City, California. 14, Paratype female, same locality.

scales, pale scales predominate on base and mesial aspect, 3rd segment darker and often pale at tip; male maxillary palpus extends nearly to ½ length 2nd segment labial palpus, 1st segment thin and elongate, 2nd bulbous distally, pale tufts of elongate thin scales from 2nd and 3rd segments extend to distal aspect 2nd segment labial palpus, female maxillary palpus short, 3rd segment reduced, scale tufts shorter; tongue well developed, covered proximally with gray and pale scales; antenna laminate, basal 5–6 segments of male flagellum modified forming a mesial sinus, first several segments of sinus may be fused or partially fused, each modified segment with a distal spine, spines progressively larger distally, sinus bordered medially and laterally by rows of gray and pale-tipped gray scales, inner row of scales forming medial border of sinus modified, thick, dark, each with curved central spine-like tooth, base female flagellum unmodified, unmodified segments of flagellum in both sexes scaled with fine bands of gray and pale scales, scape with broad posterior band of pale scales. *Thorax:* Dorsum, tegula, and collar scaled with pale-tipped gray scales, whitish scaling predominates on ventral thorax; legs scaled with mixture of gray and whitish scales, white predominates on mesial aspect, mesotibia with dark band at ⅔rds, metatibia sometimes with vague darker banding, tarsi contrastingly dark, each segment white-tipped distally, protibia with spine-tipped epiphysis from middle extending just distal to first tarsal joint, mesotibia with one and metatibia with two pair of spurs. *Wings* (Figs. 13–14): Forewing pale gray with little variation, pale scales nearly uniformly distributed in basal, medial, and subterminal spaces, often a vague darker patch at anal margin of median space; antemedial line slightly paler than rest of wing, oblique, variably dentate, indented and most contrasting in lower third, margined proximally by dark gray patch along lower third, and distally by a darker line which is widest at costal half; postmedial line pale, dentate, indented opposite cell and in lower third, margined proximally and distally by dark line, the proximal dark line usually better defined; terminal line a thin row of dark gray spots; discal spot dark gray, bilobed; fringe pale gray white-tipped scales; underside pale gray, paler along inner margin, weakly developed dark subterminal mark at costa, terminal line faint. Hindwing pale brownish gray, slightly translucent, darker at outer margin, veins slightly darkened; fringe contrasting, pale, a brownish gray band proximal third; underside light gray, slightly darker at costal and outer margins. *Abdomen:* Scaled with gray and whitish scales forming lighter bands at posterior margin of segments.

Male genitalia (Figs. 1–3): Uncus subtriangular, hood-like; gnathos with a stout central hook; valva with base broad and concave mesially, flattened and tapering distally, proximal ¾ costa slightly thickened and with small smooth bulge at base, saccular margin thickened in proximal ½ and forming a bulbous rounded basal protuberance; clasper (*sensu* Heinrich) large, arising from base of valve as a thick heavily sclerotized hollow spine, midportion slightly incurved, pointed distally, ⅓–½ length of valve, basal portion finely spiculate; tegumen unmodified; juxta U-shaped, forming a pocket anteriorly, posterolateral paired processes slightly incurved, often with a short spine at tip of each process; aedeagus (Fig. 3) slightly keeled ventrally, divided distally, divisions symmetric, sclerotized, each division with a single short ventrolateral rose thorn-like process proximal to posterior end, cornuti absent; anellar membrane developed into wrinkled membranous folds mesial to valve base; eighth abdominal sternite sclerotized as in Fig. 2 with prominent hair pencils.

Female genitalia (Fig. 4): Ostium bursae large, rectangular, nearly equal in length to corpus bursae, lamella postvaginalis largely membranous with weakly developed bands of sclerotization, lamella antevaginalis developed into paired, convoluted, heavily sclerotized plates with broadly rounded posteromedial margins, anterior aspect of ostium bursae produced into a squared-off pocket which protrudes dorsal to ductus bursae; junction of ostium bursae and ductus bursae membranous, flanked internally by fleshy folds; ductus bursae short, membranous, about ⅔ width of corpus bursae, a slightly asymmetric bulge on left; corpus bursae membranous, broadest in anterior half, nearly symmetric; ductus seminalis dorsal, from posterior margin of corpus bursae; ovipositor telescoped, less than half length of genital capsule, ovipositor lobes slightly rounded laterally.

Holotype.—♂ (Fig. 13), California, Placer Co., Ward Creek, 2 mi S. Tahoe City, 6,050′, 28 July 1980, N. Westerland (LACM). [This locality is actually at 6,250′ elevation per J. D. Donahue, personal communication 1999.]

Paratypes [LACM, UCB, NMNH].—96 ♂, 52 ♀. CALIFORNIA: Placer Co., Ward Creek, 2 mi S. Tahoe City, 6,050′, N. Westerland (LACM) [This locality is actually at 6,250′ elevation per J. D. Donahue, personal communication 1999.]: 1 ♂, 21 Jun 1974; 2 ♂, 29 Jun 1974; 1 ♂, 14 Jul 1974;

1 ♂, 21 Jul 1974; 1 ♀, 22 Jul 1974; 1 ♂, 2 Aug 1974; 1 ♂, 8 Jul 1975; 1 ♂, 17 Jul 1975; 1 ♂, 22 Jun 1979; 1 ♂, 25 Jul 1979; 1 ♂, 29 Jul 1979; 2 ♀, 7 Aug 1979. Placer Co., Ward Creek, 2 mi S. Tahoe City, 6,250′, N. Westerland (LACM): 1 ♂, 15 Jun 1966; 1 ♀, 9 Jul 1976; 1 ♂, 10 Jul 1976; 1 ♂, 12 Jul 1976; 2 ♀, 21 Jul 1976; 1 ♂, 28 Jun 1977; 1 ♀, 15 Jul 1977; 1 ♂, 17 Jul 1977; 1 ♀, 19 Jul 1977; 1 ♀, 22 Jun 1978; 1 ♂, 9 Jul 1978; 2 ♀, 15 Jul 1978; 1 ♂, 17 Jul 1978; 1 ♂, 19 Jul 1978; 1 ♂, 26 Jul 1978; 1 ♀, 3 Aug 1978; 1 ♂, 18 Jul 1979; 1 ♂, 24 Jul 1979; 1 ♂, 5 Jul 1980; 1 ♂, 16 Jul 1980; 1 ♂, 24 Jul 1980; 1 ♂, 25 Jul 1980;1 ♂, 27 Jul 1980; 1 ♂, 1 ♀, 29 Jul 1980; 1 ♂, 1 ♀, 30 Jul 1980; 1 ♂, 1 ♀, 4 Aug 1980; 1 ♀, 8 Aug 1980; 2 ♂, 24 Aug 1980; 1 ♂, 22 Jun 1981; 2 ♂, 25 Jun 1981; 1 ♀, 26 Jun 1981; 1 ♀, 29 Jun 1981; 1 ♀, 3 Jul 1981; 1 ♂, 5 Jul 1981; 1 ♀, 20 Jul 1981; 1 ♂, 26 Jul 1981; 1 ♂, 28 Jul 1981; 1 ♂, 3 Jul 1982; 1 ♂, 8 Jul 1982; 1 ♂, 10 Jul 1982; 1 ♂, 1 ♀, 14 Jul 1982; 1 ♂, 20 Jul 1982; 1 ♀, 23 Jul 1982; 1 ♂, 24 Jul 1982; 1 ♂, 25 Jul 1982; 1 ♂, 26 Jul 1982; 1 ♂, 1 ♀, 27 Jul 1982; 2 ♂, 28 Jul 1982; 1 ♀, 1 Aug 1982; 1 ♂, 7 Aug 1982; 1 ♂, 10 Aug 1982; 1 ♀, 8 Aug 1982; 2 ♀, 16 Aug 1982; 1 ♀, 22 Aug 1982; 1 ♂, 30 Jul 1983; 1 ♂, 4 Aug 1983; 1 ♂, 8 Aug 1983; 1 ♂, 5 Jul 1984; 1 ♂, 12 Jun 1985; 1 ♀, 28 Jun 1985; 1 ♂, 30 Jun 1985; 1 ♂, 2 Jul 1985; 2 ♂, 3 Jul 1985; 1 ♂, 6 Jul 1985; 1 ♂, 9 Jul 1985; 1 ♀, 14 Jul 1985; 1 ♀, 17 Jul 1985; 1 ♂, 26 Jul 1985; 1 ♂, 6 Jul 1986; 1 ♂, 7 Jul 1986; 1 ♀, 12 Jul 1986; 1 ♂, 1 ♀, 13 Jul 1986; 1 ♂, 14 Jul 1986; 1 ♂, 1 ♀, 15 Jul 1986; 1 ♀, 4 Aug 1986; 2 ♂, 1 ♀, 13 Aug 1986; 1 ♀, 20 Aug 1986; 1 ♂, 17 Jun 1987; 1 ♂, 29 Jun 1987; 1 ♀, 30 Jun 1987; 2 ♀, 9 Jul 1987; 1 ♀, 11 Jul 1987; 1 ♂, 16 Jun 1988; 1 ♀, 3 Jul 1988; 1 ♂, 5 Jul 1988; 1 ♂, 9 Jul 1988; 1 ♂, 11 Jul 1988; 1 ♀, 12 Jul 1988; 1 ♂, 16 Jul 1988; 1 ♀, 17 Jul 1988; 1 ♀, 20 Jul 1988; 2 ♀, 22 Jul 1988; 2 ♂, 26 Jul 1988; 1 ♂, 24 Jun 1989; 1 ♂, 4 Jul 1989; 2 ♂, 5 Jul 1989; 1 ♂, 13 Jul 1989; 1 ♂, 16 Jul 1989; 1 ♀, 22 Jul 1989; 1 ♀, 23 Jul 1989; 1 ♀, 27 Jul 1989; 2 ♂, 26 Jul 1990; 1 ♀, 11 Jul 1991; 4 ♂, 1 ♀, 16 Jul 1991; 1 ♂, 19 Jul 1991; 1 ♂, 21 Jul 1991; 1 ♂, 23 Jul 1991; 1 ♂, 5 Aug 1991; 1 ♂, 11 Aug 1991. Placer Co., Ward Creek, 4 km S of Tahoe City, 1 ♂, 12-VII (UCB). OREGON: Crook Co., Ochoco N. F[ore]st, 1 ♂, July 3, 1967, J. H. Baker (NMNH).

Discussion.—Remarkably, all specimens examined, with the exception of one specimen from central Oregon (not mapped), were collected at the type locality. The type locality, the previous retirement home of the late Nils Westerland, is 2–3 blocks from the northwest shore of Lake Tahoe and within the mixed conifer forest of the eastern Sierra Nevada. Common conifers include *Abies concolor* (Gordon & Glend.) Lindley, *Pinus jeffreyi* Grev. & Balf., and *Pinus contorta* Loudon. Shrubs noted in the vicinity of the Westerland home include *Ceanothus cordulatus* Kellogg, *Symphoricarpos* sp., *Cornus* sp., *Epilobium* sp., *Amelanchier* sp., *Lonicera* spp., and *Ribes* spp. (Julian P. Donahue, personal communication 1996). Nils Westerland collected insect specimens intensively at the type locality from 1973 to 1991 with most moths collected at a blacklight sheet operated on his back porch. He collected representative samples for the LACM each night and that may account for the wide range of dates for which only one or two specimens of *P. westerlandi* are recorded. An alternative explanation is that *P. westerlandi* was infrequently encountered at the Westerland residence. Flight dates range from 12 June to 24 August with most specimens collected in July. The life history and habits of *P. westerlandi* are unknown.

Several specimens of *P. impostor* were found from the type locality of *P. westerlandi*. The drier region south of Lake Tahoe yielded several more specimens of *P. impostor* and appears to represent the more typical habitat of this species. We caution, however, that the large size of Sierra Nevadan *P. impostor,* combined with its established sympatry with *P. westerlandi,* necessitates genitalic dissection as the only reliable means to identify the new species.

Etymology.—We take great pleasure in naming this special phycitine for Nils August Westerland IV (1906–1995) to honor his persistence in securing the type series. Nils Westerland shared a long association with southern California lepidopterists and the LACM (Donahue 1988, 1996). We are further indebted to Julian Donahue for bringing this new *Pyla* species to our attention and permitting us the opportunity to describe it.

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Note.—Lerant (2001. Revue Française d'Entomologie 23(2): 129) recently described a new genus, *Mitilella*, for *Pyla fusca*. In both the description and illustration (Lerant: fig. 1), the heavily sclerotized closed division of the aedeagus is misinterpreted as a thick cornutus. Pending further phylogenetic analysis of *Pyla*, we are inclined to retain *P. fusca* in the genus *Pyla*.

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PSEUDOBRYOMIMA FALLAX (HAMPSON) AND *P. MUSCOSA* (HAMPSON) (LEPIDOPTERA: NOCTUIDAE) LEAF-MINING NOCTUIDS ON FERNS

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Abstract.—The genus *Pseudobryomima* includes three species, but these are probably congeners with the ten described species of *Properigea. Pseudobryomima fallax* (Hampson) was reared ex ovo on a fern, *Pellaea andromedifolia* (Kaulf.) Fée (Pteridaceae), and *P. muscosa* (Hampson) was reared on *Polypodium californicum* Kaulf. (Polypodiaceae) from field collected early instar larvae. Larvae began as blotch miners, but later instar larvae made shelters. The larva of *P. fallax* is described and illustrated.

Key Words: Lepidoptera, Noctuidae, Quail Ridge, California, cliff brake fern, Polypodiaceae, Pteridaceae, leaf miner

The three known species of *Pseudobryomima* Barnes and Benjamin are closely related to the ten described species of *Properigea* Barnes and Benjamin and may ultimately prove to be congeneric; all are exclusively Nearctic. None of the *Properigea* or *Pseudobryomima* has had their biology previously reported. We collected a female of *Pseudobryomima fallax* (Hampson) on the Quail Ridge Ecological Reserve, Vaca Mountains, Napa County, California, 38°29′20″N latitude and 122°08′14″W longitude, at an elevation of 440 meters. The species is illustrated by Hampson (1906: plate 105, fig. 8). The moth was retained for eggs.

On October 23, 1994, when the parental female moth was collected, we had dry fall conditions with relatively few plants that were still green. Under wet spring conditions the Quail Ridge site would have hosted several hundred available food plant candidates (anonymous 1993). The dry conditions led to the discovery of a food plant.

BIOLOGY

Upon eclosure, the first-instar larvae of *Pseudobryomima fallax* were offered a leaf from all the plants we could find in nearby Cold Canyon that were still green in November. The flora has been well documented for this region (Weathers et al. 1985, Hickman 1993). The first-instar larvae failed to feed on the following: *Achillea millefolium* L., *Aristolochia californica* Torrey, *Brickellia californica* (Torrey & Gray) A. Gray, *Ceanothus cuneatus* (Hook) Nutt., *Cercis occidentalis* Torrey, *Dryopteris arguta* (Kaulf.) Maxon, *Eriodictyon californicum* (Hook. & Arn.) Torrey, *Heteromeles arbutifolia* (Lindley) Roemer, *Lactuca* sp., *Lupinus albifrons* Benth., *Arctostaphylos manzanita* C. Parry, *Mimulus aurantiacus* Curtis, *Oxalis* sp., *Pinus sabiniana* Douglas, *Quercus douglasii* Hook. & Arn., *Rubus ursinus* Cham. & Schldl., *Salix* sp., *Sambucus mexicana* C. Pressl, and *Vitis californica Benth.* Fungi, lichens, and dead wood also were rejected. They fed only

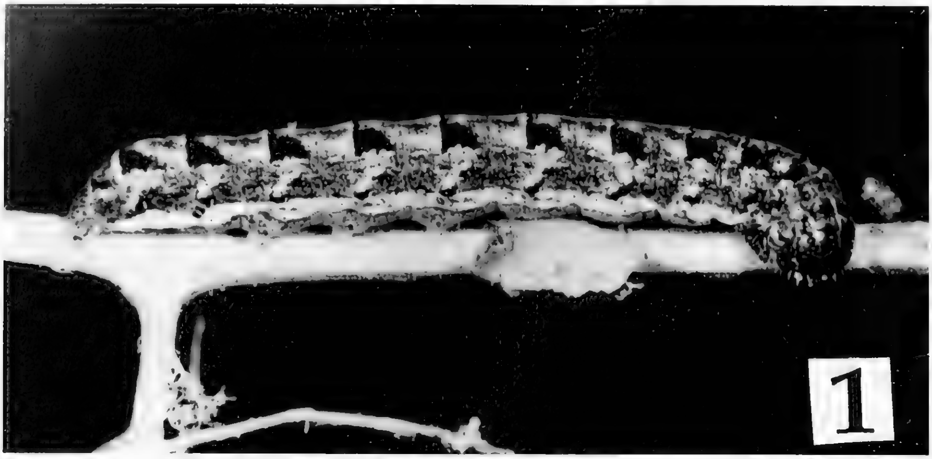


Fig. 1. *Pseudobryomima fallax*, mature larva.

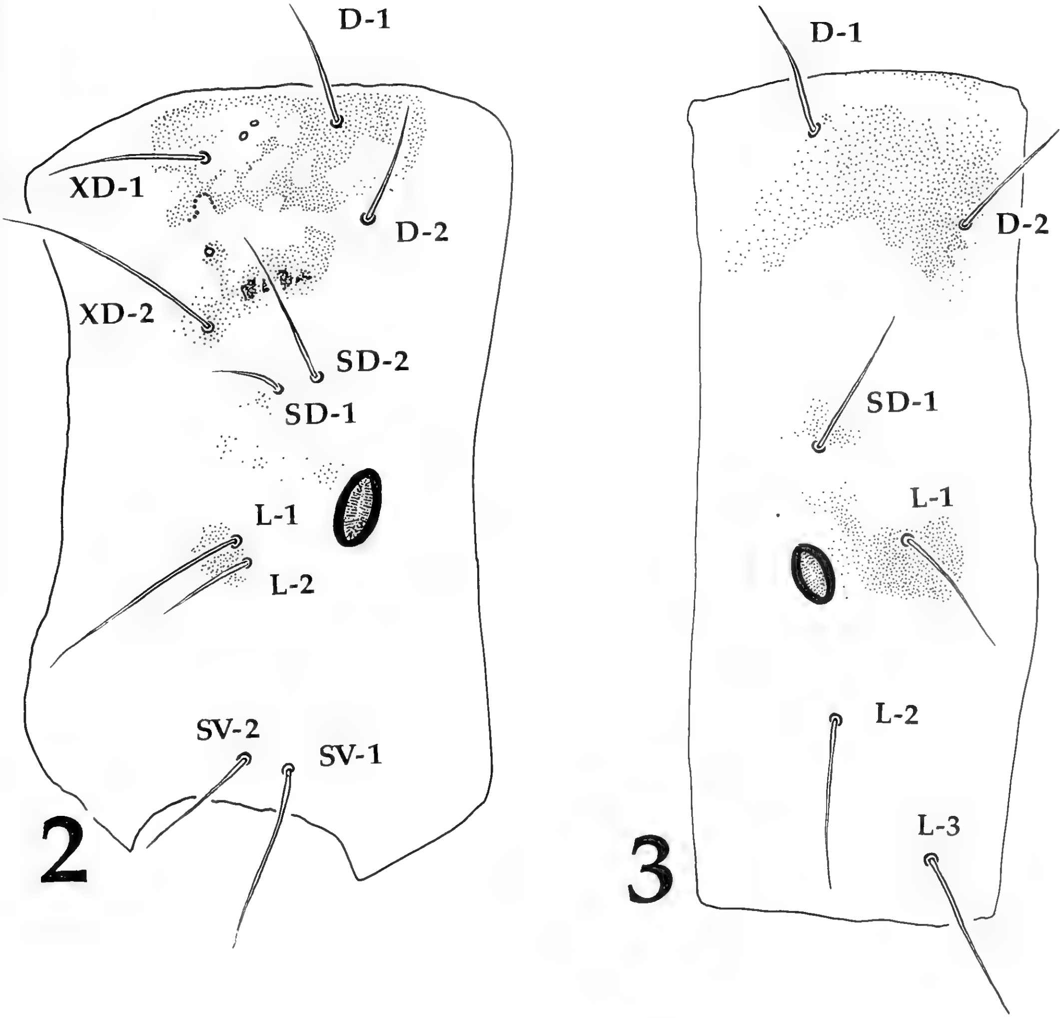
upon a cliff brake, *Pellaea andromedifolia* (Kaulf.) Fée (Pteridaceae). Last-instar larvae continued to reject higher plants from Quail Ridge, but accepted *Matteuccia struthiopteris* (L.) Todaro (Aspleniaceae) growing at the University of California, Davis, Arboretum—a fern neither native to California nor found at Quail Ridge. The first-instar larvae had rejected *Dryopteris* (Aspleniaceae) from Quail Ridge so the possibility existed that this fern specialist becomes more general in late instars, although *Dryopteris* was not offered to last-instar larvae.

The parental female of the reared brood was collected October 23, 1994. It oviposited the next day, and the ova eclosed after eight days. The first- and second-instars fed as a blotch miner, i.e., on the mesothelium of a fern pinna. Later instar larvae tied several pinnae and eventually whole fronds together and sheltered in the resulting chamber. We are unaware of any other noctuid that starts out as an internal leaf miner and switches to an external existence in a leaf shelter, although internal root- and stem-borers can start as leaf miners. The first mature larvae were acquired by December 16, 1994—the last matured by January 3, 1995.

On San Bruno Mountain (San Mateo Co., California) one of us (JD) found blotch miners on *Polypodium californicum* Kaulf. (Polypodiaceae) in 1982. Repeated visits over the next few years ultimately resulted in reared and identified adults in 1985. These were *Pseudobryomima muscosa* (Hampson).

With our discovery of the biology of two *Pseudobryomima* species, we now may be able to discover a fern specialty for *Pseudobryomima distans* (McDunnough). Subsequent to submitting this paper, one of us (TLM) visited Little St. Simon's Island in Georgia and got first-instar larvae of *Properigea tapeta* (Smith) to feed on resurrection-fern, *Polypodium polypodioides* (L.) Wyatt (Polypodiaceae). In the northeastern United States, one uncommon and localized *Properigea* species occurs in calcareous environs that also serves as *Pellaea* habitat.

Fern feeding is not commonplace among the Lepidoptera. Toxic compounds found in ferns deter herbivores. Only a few specialists, usually closely related, have been associated with these plants. It is so uncommon that the discovery of a fern host for *Pseudobryomima* suggests a closer relationship with some fern feeders than had been previously suspected. *Euplexia benesimilis* McDunnough shows a prediliction towards ferns; Palearctic *Conservula* is known from ferns; the host of *Iodepepla u-album* (Guenée) is unknown but fern is suspected. These species and *Pseudobryomima* share a



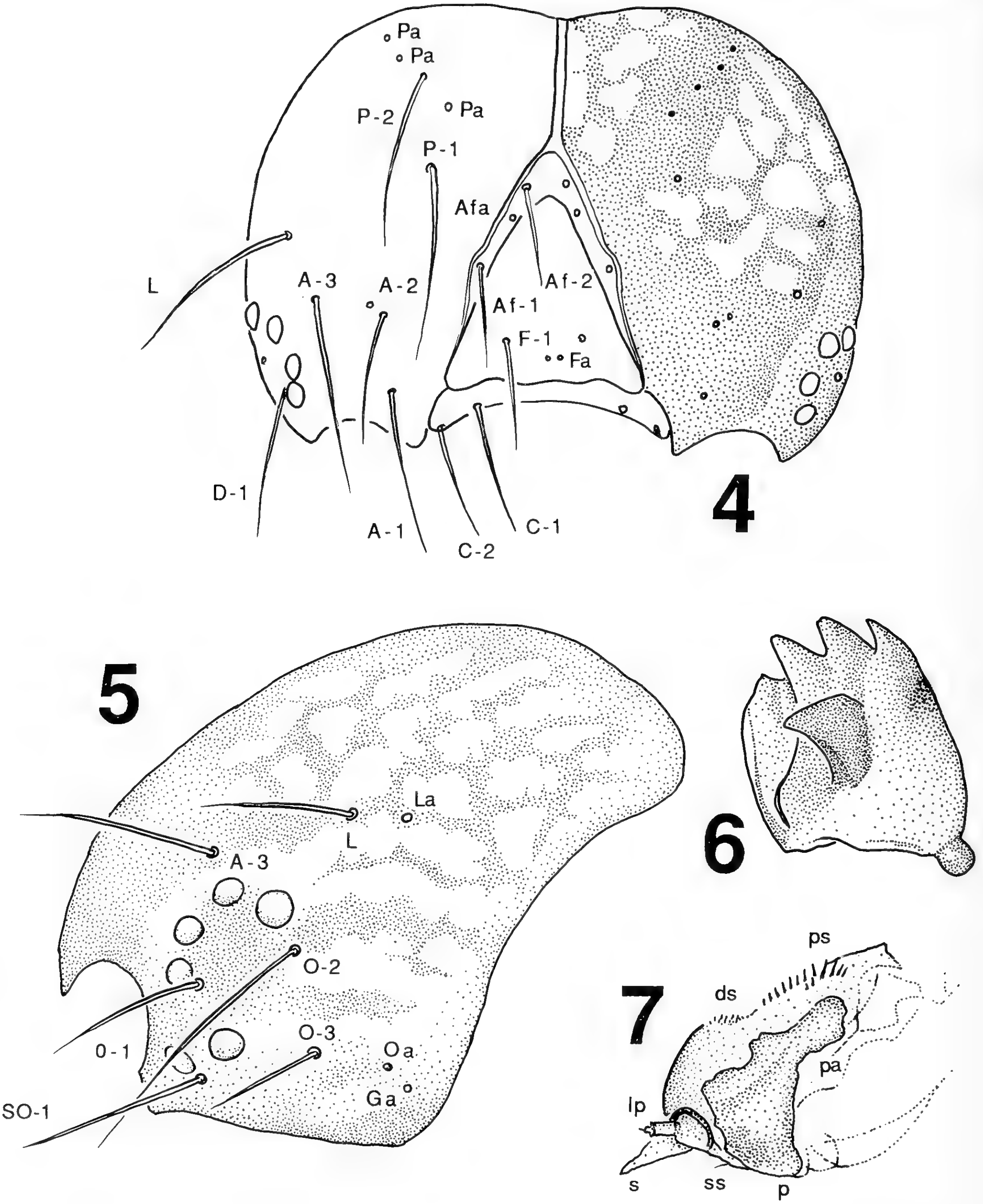
Figs. 2–3. *Pseudobryomima fallax*. 2, First thoracic segment, lateral view (anterior to left); ventral setae not shown. 3, First abdominal segments, lateral view (anterior to left); subdorsal setal base only (seta lacking, base reduced); subventral and ventral setae not shown. Abbreivations: D-1, D-2 = dorsal setae; XD-1 & 2 = primary setae; SD 1 & 2 = subdorsal setae; L1 & 2 = lateral setae; Sv-1 & 2 = subventral setae.

distinctive vesical feature, a bulbed cornutus bearing a rather long spine. *Callopistria* spp., *Fagitana littera* (Guenée), and several species of *Papaipema* have fern specialists, but appear to be more distant based on genitalic features. General feeders will sometimes tolerate ferns, particularly in the last instar.

The parental female and preserved larvae are brood-coded "tlm 94-78." Preserved larvae are vouchered in the New York State Museum, the Bohart Museum, U.C. Davis, and the Essig Museum of Entomology, U.C. Berkeley.

LAST INSTAR LARVA OF *PSEUDOBRYOMIMA FALLAX*

Description.—Gray brown with bold, black, subdorsal wedges connected across dorsum by a narrow black line along posterior margin of segment (Fig. 1). Below each subdorsal wedge a paler wedge that tapers to spiracle. Light brown spiracles partially imbedded in lateral dark markings



Figs. 4–7. *Pseudobryomima fallax.* 4, Head capsule, frontal aspect. Drawn to show setae and head pattern separately. For accurate ocellar arrangement see Fig. 5. 5, Head capsule, lateral aspect. 6, Oral face of left mandible showing mesal tooth. 7, Hypopharyngeal complex. Abbreviations: Pa = posterior head punctures; P-1 & P-2 = posterior head setae; L = lateral head seta; A1, 2 & 3 = anterior head setae; O-1 = ocellar seta; Af-1 & 2 = adfrontal setae; Afa = adfrontal puncture; F-1 = frontal seta; Fa = frontal puncture; C-1 & C-2 = clypeal setae. La = lateral puncture; L = lateral seta; A-3 = anterior head setae; O-1-3 = ocellar setae; Oa = ocellar puncture; Ga = genal puncture. Ps = proximolateral spines; Ds = distal spines; Lp = labial palpus; S = spinneret; Ss = stipular seta; P = prementum; Pa = premental arm.

(Figs. 1, 3). A broad, subspiracular, white stripe present. Integument smooth. Normal setae present; SD-2 (second subdorsal) setal base represented by a faint puncture on abdominal segments. Average body length 26 mm, but larvae probably undersized as a result of less than optimal rearing conditions. Head: Intricately patterned with light areas along frontal suture and on sides of head between coronal punctures and ocelli (Figs. 4, 5). Mandible: Three prominent teeth, fourth and fifth teeth as a low ridge. A large mesal tooth present (Fig. 6). Hypopharynx: Spinneret twice as long as labial palpus. Fine distal spines and an uneven row of 12 to 14 stout proximolateral spines present. Premental arm blunt posteriorly. Prolegs and crochets: Prolegs present and well developed on abdominal segments 3–6 and 10. Crochets average 29 on Abd-3; 30 on Abd-4; 32 on Abd-5; 32 on Abd-6; 36 on Abd-10; arranged in a uniordinal homoideous mesoseries (N = 14).

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We thank Dr. Lynn Kimsey and Dr. Steve Heydon for extensive use of the facilities of the Bohart Museum of Entomology, University of California, Davis, during the fall and winter of 1994. We also thank Dr. Grady Webster of U.C. Davis for the fern determination, Ms. Patricia Kernan for the technical drawings, Mr. Frank Maurer of the Quail Ridge Wilderness Conservancy for encouraging the Lepidoptera survey and the University of California Natural Reserve System for permission to conduct the survey, and Ms. Carin Berolzheimer for permission to collect and accommodations on Little St. Simon's Island in Georgia. Collections of *P. muscosa* at San Bruno Mt. County Park were conducted with permits issued by the San Mateo County Park Department. Dr. J. D. Lafontaine and an anonymous reviewer made constructive comments on the manuscript.

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LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *OXYNA ATERRIMA* (DOANE) (DIPTERA: TEPHRITIDAE) ON *ARTEMISIA TRIDENTATA* NUTTALL (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—*Oxyna aterrima* (Doane) is a univoltine, monophagous, circumnatal tephritid reproducing in galls of terminal and axillary buds on terminal branches of *Artemisia tridentata* Nuttall. The first-, second-, and third-instar larvae, and puparia are described and figured. *Oxyna utahensis* Quisenberry is synonymized with *O. aterrima* on the basis of morphology and concurrent rearings of flies that would key to both names from the same type of galls on the same host-plant individuals. The third instar of *O. aterrima* is distinguished from other known Tephritinae by the verruciform sensilla surrounding each posterior spiracular plate dorsolaterally, laterally, and ventrolaterally, and by the pair of verruciform sensilla comprising each intermediate sensory complex. Oviposition occurs in spring (May–June) and the first instars pass the summer (June–September) singly in small, basal, ovoidal cells within the slow-growing, small, clavoidal, uniloculate, bud gall. Second instars occupy their still-small chambers until early winter (December), when they molt to third instars, that then overwinter and grow slowly until the resumption of the spring flush of new plant growth (March). At this time, the third instar enlarges the gall chamber within the still-small gall to accommodate its faster growth and fashions an apical or subapical window for adult egress. During larval growth and development the gall apparently serves as a plant nutrient-sink to which the largely liquid diet of the larva is translocated. Pupariation follows in early April, and adults emerge by mid-April. Adults on average are short-lived (ca. 2–3 weeks). Mating behavior is described. *Mesopolobus* sp. and *Pteromalus* sp. (Hymenoptera: Pteromalidae) and a single individual of *Eupelmus* sp. (Hymenoptera: Eupelmidae) were individually reared from third instars or puparia of *O. aterrima* as solitary, larval and/or pupal ectoparasitoids. Predation by birds, probably bushtits, *Psaltriparus* sp., also is reported.

Key Words: Insecta, *Oxyna,* Asteraceae, *Artemisia,* nonfrugivorous Tephritidae, synonymy, adult taxonomy, biology, taxonomy of immature stages, galls, circumnatal life cycle, plant nutrient sinks, mating behavior, parasitoids, bird predation

This paper treats *Oxyna aterrima* (Doane) (Diptera: Tephritidae) as the first of two papers on the two species of *Oxyna* known from North America (Foote et al. 1993). My next paper will treat *O. palpalis* (Coquillett). A third species name, *O. utahensis* Quisenberry (Foote et al. 1993), is synonymized herein with *O. aterrima.*

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of terminal branches and galls on *Artemisia tridentata* Nuttall prob. ssp. *parishii* (A. Gray) H. M. Hall and Clements (Asteraceae) collected mainly in the area surrounding the parking lot at Devil's Punchbowl County Park;

1,372-m elevation; Township 4N, Range 9W, Section 19; Los Angeles Co., during 1995 to 1996. Excised terminal branches bearing old empty galls, eggs, and early-instar larvae, and later in the year, recognizable galls containing later instars and puparia were sampled monthly from gall-bearing plants during 1995 and 1996. Samples were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Sixteen first-, 18 second-, and 19 third-instar larvae and nine puparia dissected from galls were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia in excised, opened galls were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Central Facility for Advanced Microscopy and Microanalysis, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages mainly were used for studies of longevity in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Three such cages each containing a sexually mature male and female and an excised branch inserted in the wick were used to study oviposition. Thirteen pairs of virgin flies, each consisting of a male and a female obtained from emergence cages also were held in a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plants names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b, c, d, 2001), Goeden and Headrick (1999), Goeden and Norrbom (2001), Goeden and Teerink (1997), Teerink and Goeden (1999), and earlier works cited therein. Means ± SE are used throughout this paper. Digital photographs used to construct text figures were processed with Adobe Photoshop® Version 6. Twenty reared specimens of each sex have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). All remaining voucher specimens and reared parasitoids of this tephritid reside in my research collections.

RESULTS AND DISCUSSION

Adult.—*Oxyna aterrima* originally was described as a *Eurosta* by Doane (1899) from a single female from Colorado. Knowlton and Harmston (1937) reported it from Utah as *Tephitis aterrima,* which Quinsenberry (1949) corrected in his revision of *Oxyna,* in which he redescribed the holotype based on its examination by M. T. James, and an additional female provided to him by J. M. Aldrich. He also described *O. utahensis* Quisenberry as a separate species. Both species were listed from California by Foote and Blanc (1963) and included by Foote et al. (1993) in their seminal handbook.

I examined 135 specimens in my collection, 72 males and 63 females, most of which were reared singly with their setation intact from individual galls collected from *A. tridentata.* I found no specimens with all-yellow or all black-femora. The extremes represented in the key character separating *O. utahensis* from *O. aterrima,* respectively, i.e., "femora black except narrowly at apices" versus "femora yellowish with a black spot or strip at the base ventrally and sometimes some black dusting dorsally" in Foote et al. (1993: 259) proved inadequate to separate most of these specimens. Although 58 specimens (43%), 24 males and 34 females, have mostly dark brown or black femora narrowly yellow at apices, the rest show all possible variations in dark patterning on a yellow base color culminating in a dark, subapical, ventral spot on the middle and hind femora on two females and one male, with the fore femur mostly yellow except for a light brown ventral stripe. Thus, the color patterning of the femora of these 135 specimens is best described as: most femora with dark brown to black markings on a yellow base color. The hind femur usually is more darkly marked than the front or mid femora, either of which can be less darkly marked than the other. These markings range from the dark, apical, ventral spot noted above to a ventral streak the length of the femur, which in other specimens wrap around this segment sub-basally, then progress distad as a dorsal streak of different lengths. These longitudinal streaks then coalesce laterally on flies with mostly dark brown or black femora. Sometimes, this coalescence occurs incompletely as bands, or the ventral streak may be interrupted one or more times, both variations of which result in spotting or mottling. The front femur may be yellow distally and darkly dusted basally, and thus differently patterned from the middle and hind femora. Thus, based on this character alone, it would appear—though this is highly unlikely—that both of these "species" of *Oxyna* were reared concurrently from the same type of galls collected in some cases from the same individuals of *A. tridentata* at the same location.

The wing pattern of *O. aterrima* closely resembles that of *O. utahensis,* in that in both species a transverse hyaline area distad of vein dm-cu that extends from the costa to the posterior margin and is composed of about eight partially merged hyaline spots with some dark areas remaining between them (Foote et al. 1993; Fig. 303, p. 260). But, here again, the 135 reared flies show both wing patterns plus other wing patterns intermediate to these patterns as well as hyaline spots more intensely merged than in *O. aterrima* and less intensely merged than in *O. utahensis.* Again, based on currently employed wing characters, these adults concurrently reared from the same type of galls on the same plants could not be separated morphologically. Therefore, *O. utahensis* is synonymized with *O. aterrima,* the name having precedence, as noted above.

Further examination of the 135 specimens also tempered the following statement in Foote et al. (1993: 259):

> "The genus is always recognizable by the presence of only a single pair of black frontal bristles, a character not present in any other North American fruit fly genus. These dark frontals are always accompanied by a small group of slightly more robust, light-colored setae situated on a level with the dark bristle or anterior to it, or one light-colored seta anterior to and one posterior to the dark bristle; at least one of these light bristles is usually almost as long as the dark one . . ."

Sixteen (22%) of the 72 males examined and 11 (17.5%) of the 63 females lacked black frontal setae. An additional eight (11%) of the 72 males had only one black frontal seta; the other frontal seta was light-colored or white. Among the 63 females, seven (11%) also had a single black frontal seta. Two males (3%) and one female (1.5%) each had a pair of light-colored frontal setae. Two males (3%) and two females (3%) each had two pairs of black frontal setae; whereas, one female (1.5%) had a single black seta on one side of its head and two black frontal setae on the other side.

Immature stages.—The first-, second-

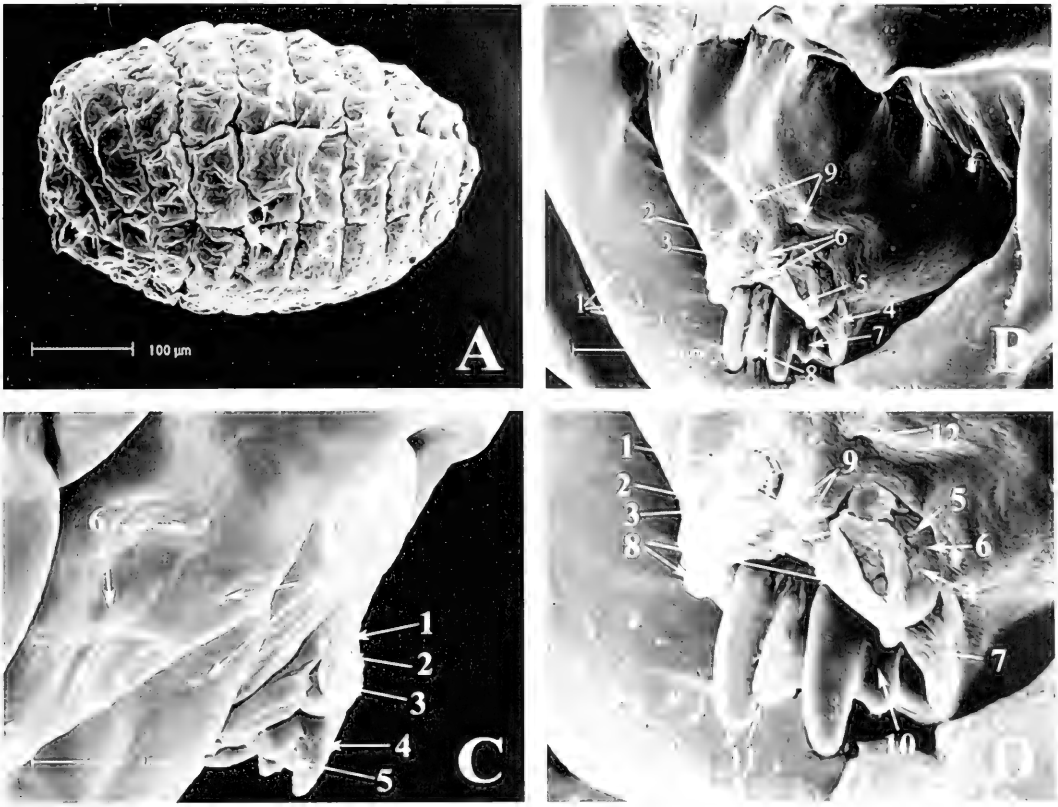

Fig. 1. First instar of *Oxyna aterrima:* (A) habitus, anterior to left; (B) gnathocephalon, frontolateral view, 1—minute acanthae, 2—anterior sensory lobe, 3—terminal sensory organ, 4—stomal sense organ, 5—lateral integumental petal, 6—medial integumental petals, 7—mouthhook, 8—median oral lobe; (C) gnathocephalon, lateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—mouthhook, 5—median oral lobe, 6—paired verruciform sensilla; (D) gnathocephalon, detail of frontal view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—stomal sense organ, 8—lateral integumental petals, 9—medial integumental petals, 10—mouthhook, 11—median oral lobe.

and third-instar larvae, and puparium are described below.

Egg: Nine eggs dissected from field-collected flower heads were white, opaque, smooth, ellipsoidal, 0.51 ± 0.02 (range, 0.42–0.58) mm long, 0.23 ± 0.01 (range, 0.20–0.24) mm wide, smoothly rounded at basal end, with a buttonlike pedicel at anterior end.

First instar larva: White, ovoidal, flattened anteriorly and less so posteriorly (Fig. 1A); body segments well-defined, integument finely wrinkled dorsally and ventrally, with sparse, hemispherical or posteriorly-directed, claviform, minute acanthae (Fig. 1B-1) on intersegmental areas of thorax and abdominal segments A1 and A2; gnathocephalon smooth, conical (Figs. 1B, C); dorsal sensory organ, well-defined, flat pad (Figs. 1B-2, C-1, D-1); anterior sensory lobe (Figs. 1B-3, C-2, D-2) bears terminal sensory organ (Figs. 1C-3, D-3), lateral sensory organ (Fig. 1D-4), supralateral sensory organ (Fig. 1D-5), and pit sensory organ (Fig. 1D-6); stomal sense organ reduced to two verruciform sensilla ventrolaterad of terminal sensory organ (Figs. 1B-4, D-7) and fused with flattened, protrudent, lateral integumental petal (Figs. 1B-5, D-8) above each mouthhook, two medial, papillate, integumental petals in vertical rows between anterior sensory lobes (Figs. 1B-6, D-9); mouthhook tridentate (Figs. 1B-7, C-4, D-10); median oral lobe laterally compressed, apically rounded (Figs. 1B-8, C-5, D-11); pore above each dorsal sensory organ (Figs. 1B-9, D-12); two or more pairs of verruciform sensilla in vertical rows on prothorax posterolaterad of gnathocephalon (Fig. 1C-6); anterior spiracle absent; lateral spiracular complexes not seen; caudal segment (Fig. 2A) with a stelex sensillum dorsolaterad (Figs. 2A-1, B), a verruciform sensillum laterad (Figs. 2A-2, C), and another stelex sensillum ventrolaterad (Figs. 2A-3, D) of posterior spiracular plate (Figs. 2A-4, E-1); posterior spiracular plate bears two rimae (Fig. 2E-2), ca. 0.006 mm long, and four unbranched spinose or apically toothed, interspiracular processes (Fig. 2E-3), the longest process measuring 0.005 mm; intermediate sensory complex (Figs. 2A-5, F) consists of stelex sensillum (Figs. 2E-4, F-1) and medusoid sensillum (Figs. 2E-5, F-2).

Second instar larva: Ovoidal, rounded anteriorly, truncated posteriorly (Figs. 3A, B), white with black marking on abdominal ventrum where ventrum and pleura densely covered with knoblike minute acanthae (Fig. 3B), gnathocephalon smooth, conical (Fig. 3C), circumscribed around middle with verruciform sensilla dorsolaterally, laterally, and ventrolaterally (Fig. 3C-1); dorsal sensory organ well-defined, round, flat (Figs. 3C-2, D-1); anterior sensory lobe (Figs. 3C-3, D-2) with terminal sensory organ (Fig. 3D-3), lateral sensory organ (Fig. 3D-4), supralateral sensory organ (Fig. 3D-5) and pit sensory organ (Fig. 3D-6); three, foliose, protrudent, lateral integumental petals (Fig. 3D-7) above each mouthhook (Fig. 3D-8), one pair of papillate, medial integumental petals (Fig. 3D-9) between anterior sensory organs; at least four oral ridges (Fig. 3D-10) surrounding each anterior sensory lobe, the inner, ventral, oral ridge with three ventral teeth is fused with the stomal sense organ (Fig. 3D-11); mouthhook (Fig. 3D-8) with at least two, possibly three teeth; median oral lobe laterally flattened, anteriorly rounded (Fig. 3D-12); anterior thoracic spiracle with three (Fig. 4A) short, flattened papillae; lateral spiracular complex of mesothorax consists of at least three verruciform sensilla in a vertical row posteriorad of spiracle (not shown); lateral spiracular complex of metathorax with a spiracle (Fig 4B-1) and three or more verruciform sensilla (Fig. 4B-2) in a vertical row posteriorad of spiracle; lateral spiracular complex of first abdominal segment similarly composed of a spiracle (Figs. 4C-1, D-1) and three verruciform sensilla (Figs. 4C-2, D-2) positioned as on meso- and metathorax; caudal segment obscured in prepared specimens.

Inter-instar differences noted with *O. aterrima* include the acquisition of an anterior spiracle in the second instar, the increase in the number of lateral integumental petals from one to three, and the major change involving the abdominal pleura covered with knob-like minute acanthae, the ventral part of this patch being pigmented black. The number of teeth on the mouthhooks of the second instar probably remain at three, as this number also is retained in the third instar. Unfortunately, no specimen adequately allowed viewing the caudal segment of the second instar to permit inter-instar comparisons.

Third instar larva: Pale yellow or white, ovoidal, tapering anteriorly, truncated posteriorly, distinctly segmented (Fig. 5A), short-spinose minute acanthae cover ventrum and anterior halves of pleura of abdominal segments A1-A4, but are sparse and restricted to anteroventral intersegmental areas of thoracic segments; gnathocephalon smooth, flattened dorsally, and medially cleaved by vertical groove (Fig. 5B-1); dorsal sensory organ well-defined, hemispherical (Fig. 5C-1); anterior sensory lobe bears terminal sensory organ (Figs. 5C-2, D-1), lateral sensory organ (Fig. 5C-3), supralateral sensory organ (Fig. 5C-4), and pit sensory organ (Fig. 5C-5); two oral

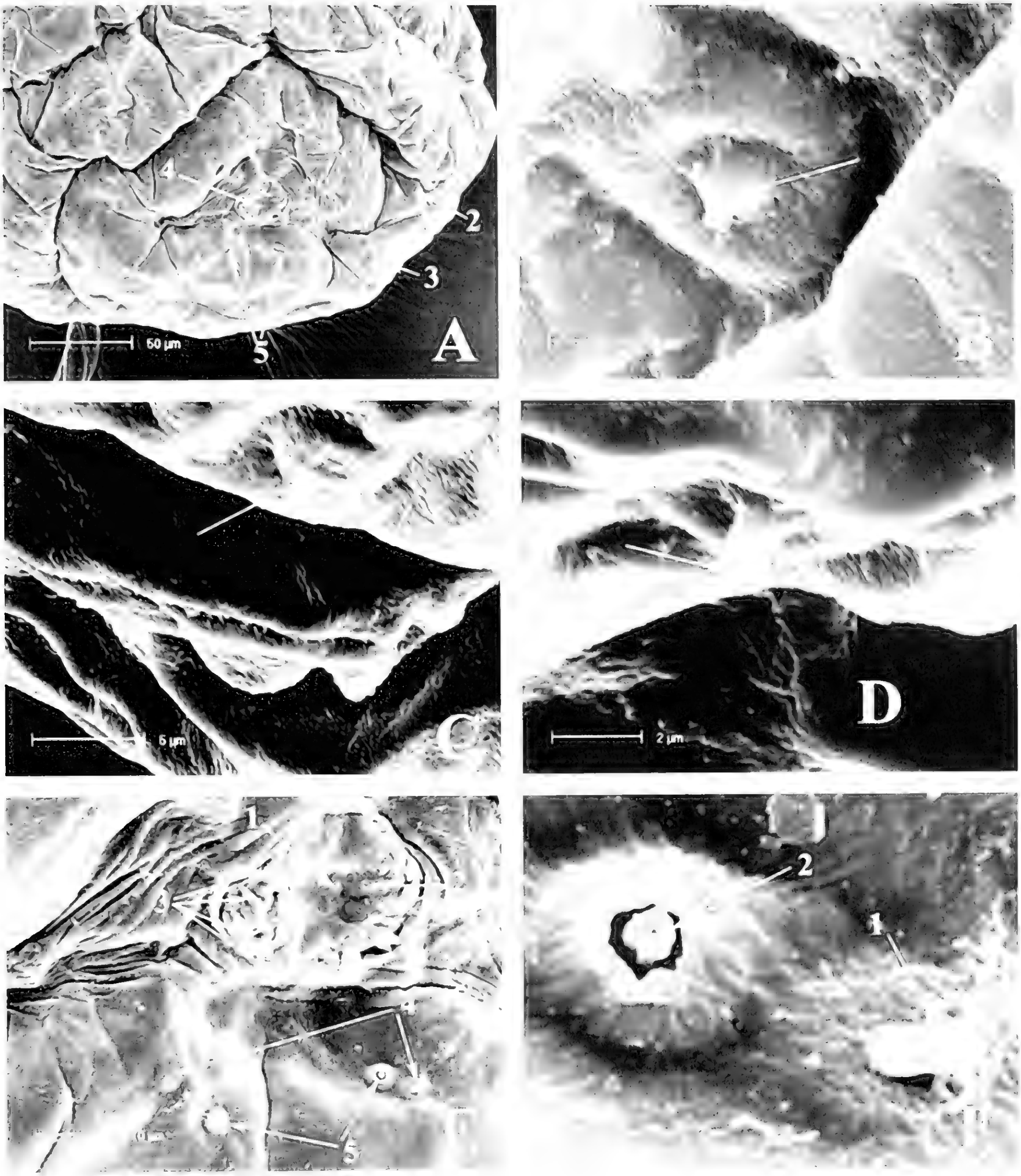

Fig. 2. First instar of *Oxyna aterrima*, continued: (A) caudal segment, 1—dorsolateral stelex sensilla, 2—lateral verruciform sensillum, 3—ventrolateral stelex sensillum, 4—posterior spiracular plate, 5—intermediate sensory complexes; (B) dorsolateral stelex sensillum (arrow); (C) lateral verruciform sensillum (arrow); (D) ventrolateral stelex sensillum; (E) 1—posterior spiracular plate, 2—two rimae, 3—four interspiracular processes, 4—stelex sensilla of two intermediate sensory complexes, 5—medusoid sensilla of two intermediate sensory complexes; (F) intermediate sensory complex, 1—stelex sensillum, 2—medusoid sensillum.

ridges (Fig. 5D-2) one laterad and one ventrolaterad of anterior sensory lobe and stomal sense organ, respectively, both lobes entire margined and separated from prominent stomal sense organ (Fig. 5D-3); mouthhook (Fig. 5C-6) tridentate (Fig. 5D-4); median oral lobe laterally flattened, apically pointed (Figs. 5C-7, D-5); three pairs

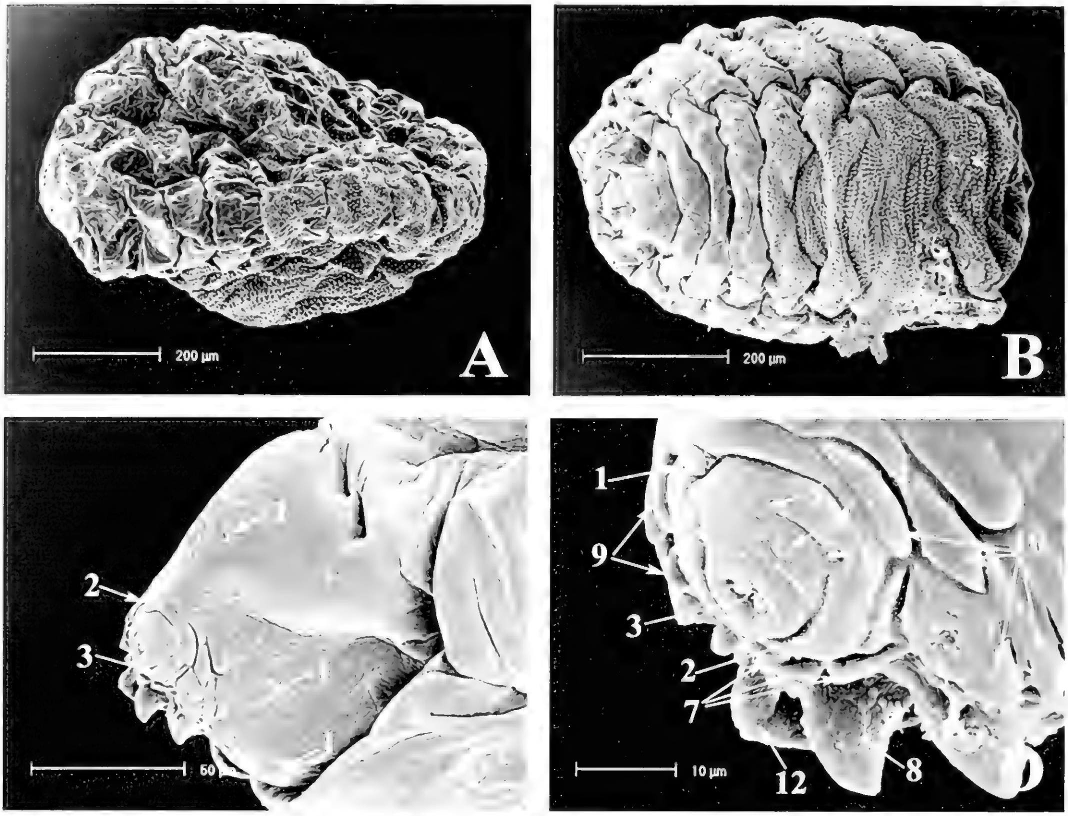

Fig. 3. Second instar of *Oxyna aterrima:* (A) habitus, anterior to left; (B) venter, anterior to left; (C) gnathocephalon, lateral view, 1—verruciform sensillum, 2–dorsal sensory organ, 3—anterior sensory lobe; (D) gnathocephalon, closeup dorsolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—lateral integumental petals, 8—mouthhook, 9—medial integumental petals, 10—oral ridges, 11—stomal sense organ, 12—median oral lobe.

medial integumental petals in vertical row between anterior sensory lobes (Fig. 5C–8), five papillate, lateral integumental petals above each mouthhook (Fig. 5C-9); labial lobe (Fig. 5D-6) broad, separated from median oral lobe anteriorally and with two pores ventrally (Fig. 5D-7); anterior thoracic spiracle with three (Figs. 5B-2, E, 6A-1) or four, hemispherical papillae (Fig. 5F); lateral spiracular complex of mesothorax consists of closed, relict spiracle (Figs. 6A-2, B-1) and four verruciform sensilla (Figs. 6A-3, B-2) in vertical row posteriorad of spiracle; lateral spiracular complex of metathorax similarly composed of spiracle (Figs. 6A-4, C-1) and four verruciform sensilla (Figs. 6A-5, D-2) similarly positioned; lateral spiracular complex of first abdominal segment similarly composed of spiracle (Figs. 6A-6, D) and four verruciform sensilla (Fig. 6A-7) in two diagonally parallel pairs; posterior spiracular plate bears three, broadly elliptical rimae, ca. 0.027 mm in length (Fig. 6E-1), and four, unbranched, spiniform, interspiracular processes, each 0.007 mm long (Fig. 6E-2); verruciform sensilla dorsolaterad, lateral, and ventrolaterad (Fig. 6F-1) of spiracular plate; intermediate sensory complex consists of two verruciform sensilla (Fig. 6F-2).

Differences noted between second and third instars include a radical change in the position, density, and shape of the minute acanthae as described above. Other changes

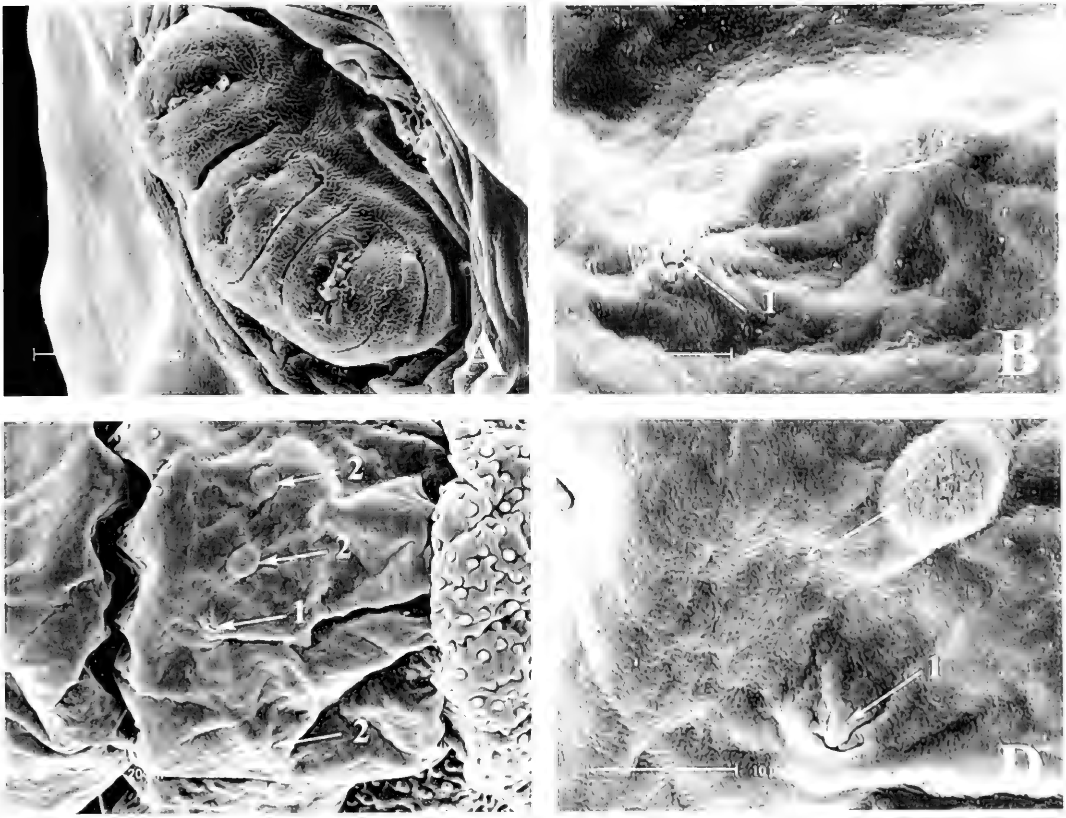

Fig. 4. Second instar of *Oxyna aterrima*, continued: (A) anterior spiracle; (B) part of lateral spiracular complex of metathorax: 1—spiracle, 2—verruciform sensillum; (C) lateral spiracular complex of first abdominal segment, 1—spiracle, 2—verruciform sensillum; (D) part of lateral spiracular complex of first abdominal segment, 1—spiracle, 2—verruciform sensillum.

include increases from three to four in the number of lateral integumental petals and from one to two pairs of medial integumental petals, plus a change in shape of the lateral petals from foliose to papillate. The anterior spiracles with three papillae in the second instar compare with three or four papillae in the third instar. The lateral spiracular complexes of the mesothorax, metathorax, and first abdominal segment of the third instar are each composed of four verruciform sensilla, rather than the three sensilla found on each of these segments in the second instar. The sensilla surrounding the posterior spiracular plate are the same in number as in the second instar; however, in the third instar all are reduced to verruciform sensilla, including the intermediate sensory complex. This is the first intermediate sensory complex composed entirely of this single, simpler form of sensillum that my coworkers and I have observed to date in our studies of larval Tephritinae.

Puparia: Reniform-ellipsoidal, black, (Fig. 7A), anterior end bears the invagination scar (Fig. 7B-1) and anterior thoracic spiracles (Fig. 7B-2); caudal segment bears posterior spiracular plates, each with three broadly elliptical, raised rimae and four, interspiracular processes (Fig. 7C-2). Dorsolateral (Fig. 7C-3), lateral (Fig. 7C-4), and ventrolateral verruciform sensilla (Fig. 7C-5) as well as intermediate sensory complexes (Fig. 7C-6), each also composed of a pair of verruciform sensilla, also present on caudal segment. Sixty-seven puparia averaged

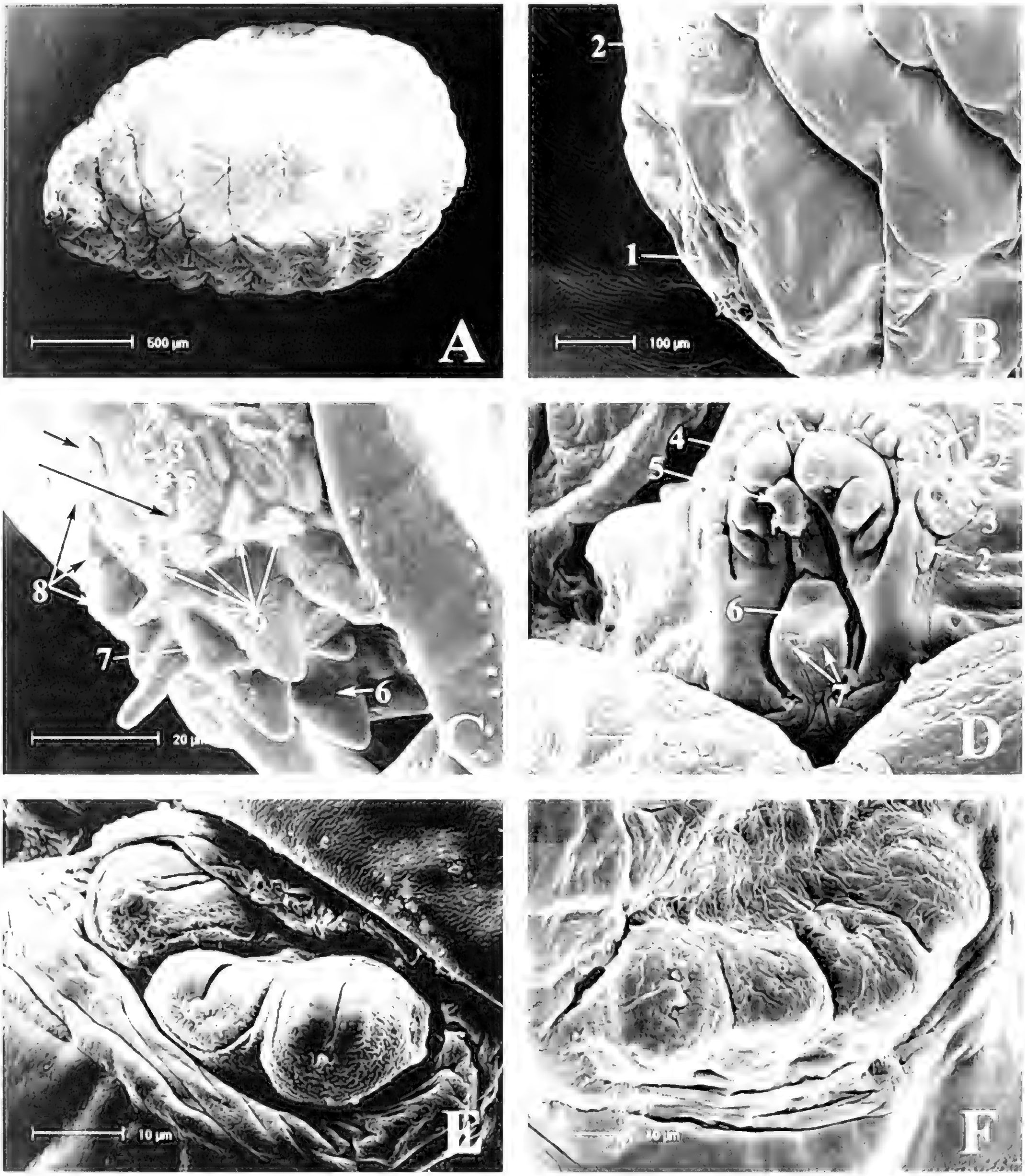

Fig. 5. Third instar of *Oxyna aterrima:* (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1—vertical groove, 2—anterior spiracle; (C) gnathocephalon, ventrolateral view, 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—supralateral sensory organ, 5—pit sensory organ, 6—mouthhook, 7—median oral lobe, 8—medial integumental petals, 9—lateral integumental petals; (D) oral cavity, ventral view, 1—terminal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—mouthhook, 5—median oral lobe, 6—paired verruciform sensilla; (D) gnathocephalon, closeup frontal view, 1—dorsal sensory organ, 2—oral ridge, 3—stomal sense organ, 4—mouthhook, 5—median oral lobe, 6—labial lobe, 7—pores; (E) anterior spiracle with three papillae; (F) anterior spiracle with four papillae.

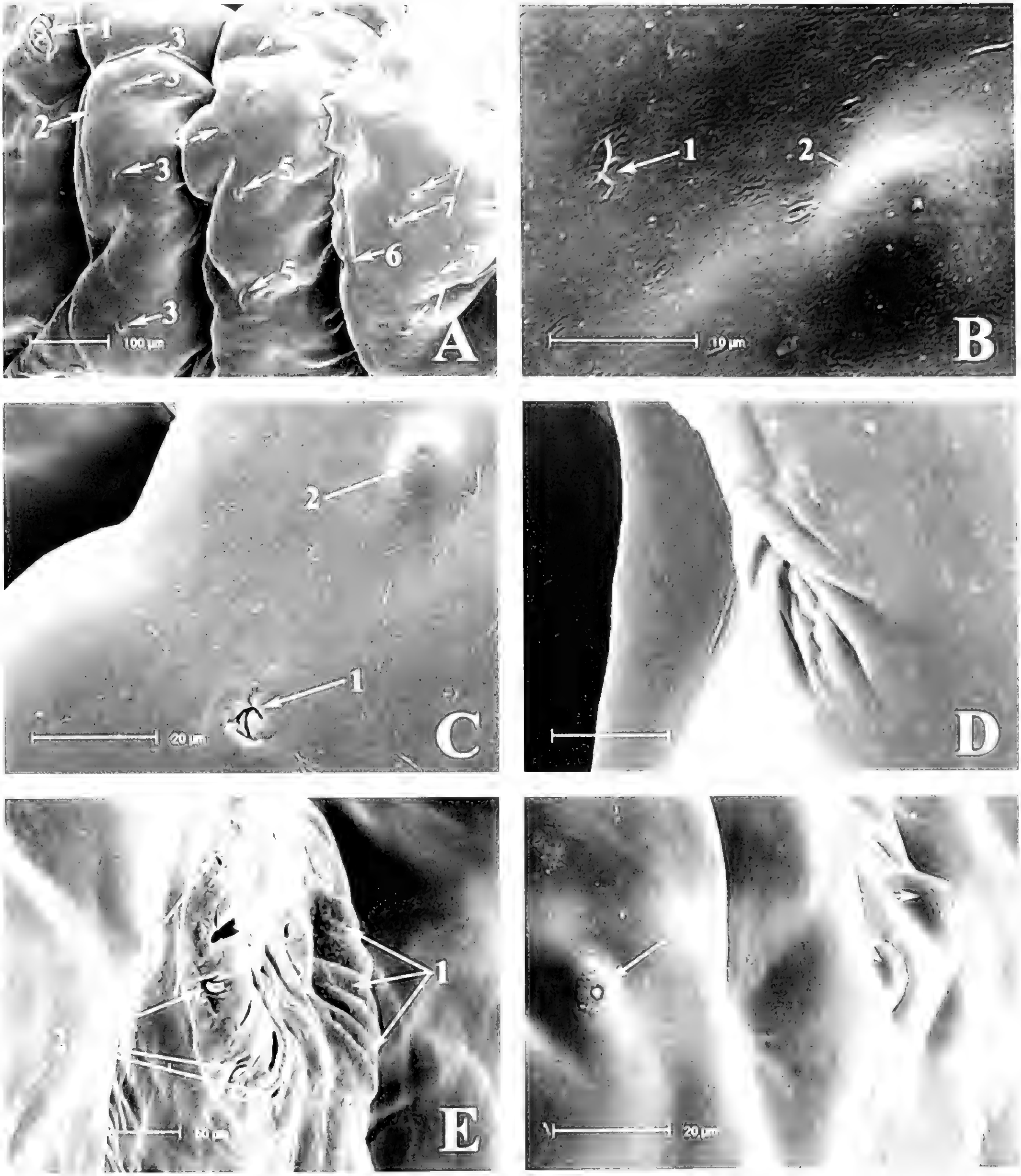

Fig. 6. Third instar of *Oxyna aterrima*, continued: (A) lateral spiracular complexes, 1—anterior spiracle, 2—metathoracic spiracle, 3—verruciform sensillum, 4—mesothoracic spiracle, 5—verruciform sensillum, 6—first abdominal segment spiracle, 7—verruciform sensillum; (B) part of lateral spiracular complex of mesothorax, 1—spiracle, 2—verruciform sensillum; (C) part of lateral spiracular complex of metathorax, 1—spiracle, 2—verruciform sensillum; (D) spiracle of lateral spiracular complex on first abdominal segment; (E) posterior spiracular plate, 1—rimae, 2—interspiracular processes; (F) 1—ventrolateral verruciform sensillum, 2—verruciform sensilla of intermediate sensory complex.

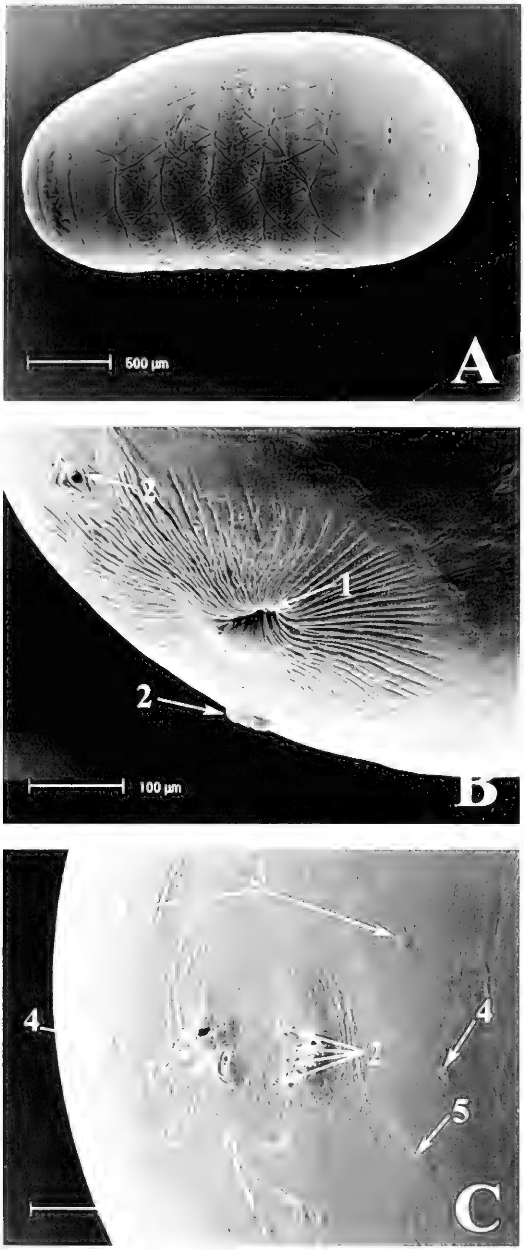

Fig. 7. Puparium of *Oxyna aterrima:* (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior spiracle; (C) caudal segment, 1—rima, 2—interspiracular process, 3—pair of dorsolateral verruciform sensilla, 4—lateral verruciform sensillum, 5—ventrolateral verruciform sensillum, 6—two pairs of verruciform sensilla comprising intermediate sensory complex.

2.87 ± 0.03 (range, 2.06–3.42) mm in length; 1.41 ± 0.014 (range, 1.14–1.92) mm in width.

DISTRIBUTION AND HOSTS

Oxyna aterrima apparently is a true monophage, with *Artemisia tridentata* as its only known host plant. This relationship was first reported for a single female determined as *O. utahensis* from *A. t.* var. *vaseyana* (Rydeberg) Beetle from Idaho by Foote et al. (1993). A composite of the distributions mapped for *O. aterrima* and *O. utahensis* in Foote et al. (1993) includes the western states of Arizona, California, Colorado, Idaho, Montana, North Dakota, Oregon, Utah, Washington, and Wyoming as well as the extreme southern parts of the Canadian provinces of Alberta, Saskatchewan, and British Columbia. Allen Norbom (in litt. 2001) also has seen specimens from the Yukon. Thus, the distribution of *O. aterrima* may coincide wholly with *A. tridentata sensu lato,* or in part with one or more of its subspecies (Hickman 1993). *Artemisia tridentata* is a shrub that inhabits dry soils, valleys, slopes from 300 to 3,000+ m in the western U.S., i.e., north to Washington, the North Central States and south to New Mexico (Hickman 1993). The distribution of *A. tridentata* also extends into southwestern Canada (Barkley 1986). However, Dodson and George (1986) demonstrated convincingly that the gall-forming tephritids *Aciurina bigeloviae* (Cockerell) and *A. trixa* Curran are less widely distributed than their host plants within four southwestern States.

BIOLOGY

Egg.—In each of 24 axillary buds or terminal buds of short axillary branches on terminal, woody, previous year's branches of *A. tridentata,* single eggs of *O. aterrima* were inserted separately, pedicel-last to depths of half to all of their lengths (Fig. 8A). Eggs were found in axillary buds or axillary branches an average of 9.5 ± 4.2 (range, 6–11.5) cm beyond the stem apices

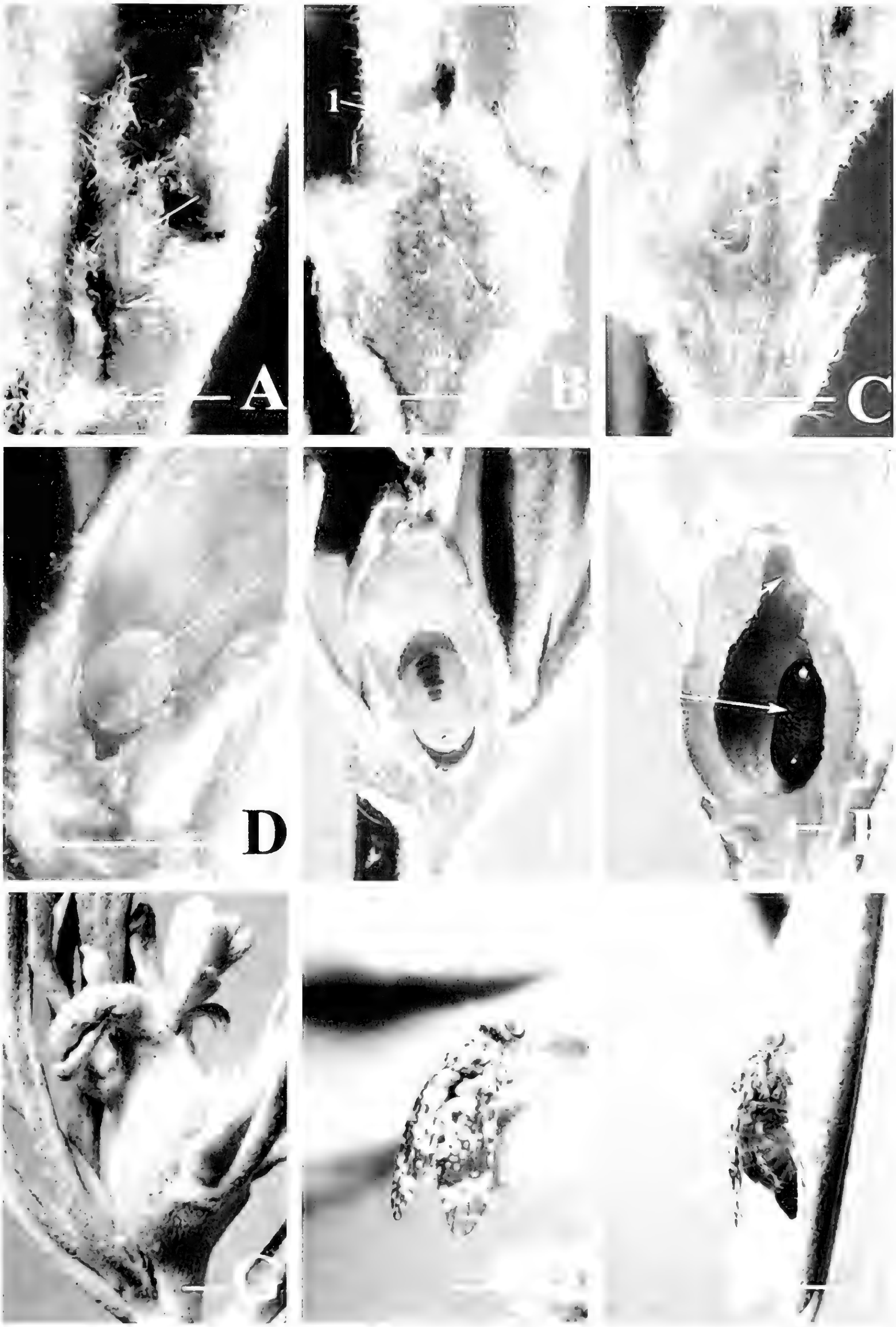

Fig. 8. Life stages of *Oxyna aterrima:* (A) egg (arrow) inserted in bud, (B) (1) empty egg chorion away from which (2) first instar tunneling into bud, (C) first instar (arrow) in cell at base of gall, (D) overwintering second instar (arrow) (note dark marking), (E) early third instar in cell in bud, (F) (1) puparium in enlarged cell with (2) exit tunnel for adult and (3) subapical epidermal window, (G) external view of gall, (H) male adult, (I) Female adult. Lines = 1 mm.

which may or may not have borne an empty, woody gall. All 24 eggs rested with their long axes parallel to the long axes of the axillary bud or branch and their pedicels pointed apicad (Fig. 8A). The diameters of these axillary buds/branches bearing eggs averaged 0.79 ± 0.08 (range, 0.55–1.49) mm. Oviposition was scattered over and throughout a stand of *A. tridentata,* not confined to certain individual host-plants galled repeatedly over successive years (Goeden 1990, Headrick and Goeden 1998).

Larva.—Bi-monthly samples of branch segments at the Devil's Punchbowl location beginning in June 1995 (Summer) showed that the embryos remained within the egg chorions for about 1–2 weeks. Upon eclosion, the first instars tunneled into the base of the axillary or terminal buds (Fig. 8B) where each remained for up to 3 months within a single, ovoidal, open, smooth-walled, basal cell (Fig. 8C). Single first instars were found in a total of 52 infested buds sampled monthly during the first 3 months following oviposition, during which time the lengths of the clavoidal galls limitedly increased in average length from 4.4 ± 1.0 (range, 3.4–5.4; n = 14) mm in mid-July to 4.9 ± 1.2 (range, 3.4–7.4; n = 12) in mid-September (early Fall). The average widths of these same galls increased from 1.78 ± 0.01 (range, 1.40–2.28) mm to 2.31 ± 0.12 (range, 1.42–3.13) mm. The cells containing the first instars averaged 0.90 ± 0.04 (range, 0.71–1.2) mm in length and 0.52 ± 0.02 (range, 0.33–0.64) mm in width in mid-July and 0.95 ± 0.06 (range, 0.71 ± 1.42) mm in length and 0.53 ± 0.02 (range, 0.36–0.57) mm in width in mid-September. Therefore, the average size of cells containing first instars remained about the same throughout the first stadium. These cells were formed at the base of each gall (Fig. 8C) an average of 2.67 ± 0.27 (range, 1.65–4.27) mm below the gall apex in July and 4.04 ± 0.41 (range, 2.85–5.70) mm in September, indicating that the gall increased in size apicad of the cell during this period.

The larva next molted to the second instar (Fig. 8D), evidenced by the cast cephalopharyngeal skeleton remaining in the cell. Two, 16, and five second instars were detected within galls sampled during mid-September (early-Fall), mid-October, and mid-November (late-Fall/early Winter). During mid-October, the external dimensions of the 16 galls containing second instars measured 4.95 ± 0.26 (range, 3.99–7.98) mm in length by 2.10 ± 0.34 (range, 1.71–2.85) in width. The ovoidal cells within these galls averaged 1.37 ± 0.40 (range, 0.64–2.28) mm in length by 0.68 ± 0.03 (range, 0.57–0.85) mm in width and were located an average of 2.76 ± 0.22 (range, 1.85–4.84) from the gall apex. Thus, the galls grew on average only slightly during the second stadium of about a month's duration as did the basal cells containing the second instars (Fig. 8C).

Development of the third instar continued slowly during the winter (Fig. 8E). Four, 15, 10, 19, 25, 20, and four third instars were found in gall samples obtained in mid-October, mid-November, mid-December, mid-January 1996, mid-February, mid-March (early Spring), and mid-April, respectively. Average exterior lengths and widths of galls containing third instars in mid-November were 4.96 ± 030 (range, 3.99–8.55) mm by 2.78 ± 0.34 (range, 1.99–3.13) mm; 5.41 ± 0.15 (range, 4.56–5.98) mm by 2.56 ± 0.09 (range, 1.99–2.85) mm in mid-December; 5.01 ± 0.14 (range, 3.99–5.84) mm by 2.22 ± 0.05 (range, 1.85–2.56) mm in mid-January 1996; 5.00 ± 0.19 (range, 3.13–6.84) mm by 2.43 ± 0.15 (range, 1.99–2.85) in mid-February; and 5.69 ± 0.20 (range, 4.56–7.98) by 3.13 ± 0.08 (range, 2.85–3.99) mm in mid-March. The length and widths of the ovoidal cells within these same galls averaged 1.68 ± 0.07 (range, 1.42–2.28) mm by 0.90 ± 0.4 (range, 0.71–1.14) mm in mid-November; 2.11 ± 0.06 (range, 1.71–2.28) mm by 1.02 ± 0.04 (range, 0.85–1.14) mm in mid-December; 1.94 ± 0.06 (range, 1.42–2.56) mm by 0.96 ± 0.03

(range, 0.71–1.14) mm in mid-January 1996; 2.05 ± 0.09 (range, 0.99–3.13) mm by 1.12 ± 0.19 (range, 3.13–1.56) mm in mid-February; and 3.16 ± 0.14 (range, 1.99–4.84) mm by 1.70 ± 0.06 (range, 1.30–2.28) in mid-March. Thus, galls and the cavities within on average increased little if any in size during the equally slow growth of the third instars during the winter. The gall cavities on average were located 2.58 ± 0.27 (range, 1.42–5.41) mm from the gall apex in mid-November; 2.65 ± 0.23 (range, 1.99–3.99) mm in mid-December; 2.27 ± 0.17 (range, 1.28–3.7) mm in mid-January 1996; 1.95 ± 0.17 (range, 0.85–3.99) in mid-February; and 1.71 ± 0.11 (range, 0.74–2.28) in mid-March, which, again, reflected the gradual increase in the size of the gall cavity and third instar within.

Pupa.—Towards the end of the third larval stadium the third instar enlarged the gall cavity to accommodate its increased size (Figs. 8E, F). The larva also ate through the gall wall leaving only a thin, round, apical or subapical, epidermal window through which the adult eventually escaped (Fig. 8F). Forty-five windows averaged 1.06 ± 0.02 (range, 0.70–1.42) mm in diameter. The fully-grown larva then pupariated with its anterior end facing the window (Fig. 8F). Three galls containing puparia were first detected in samples in mid-March (early Spring), and 50 galls sampled in early April (Figs. 8F, G) contained puparia, plus some galls were found that bore dead parasitized larvae or signs of bird predation (see section below on Natural Enemies). By mid-April, all 35 galls sampled contained empty puparia. The 50 clavoidal galls containing puparia sampled in early April externally averaged 7.23 ± 0.16 (range, 3.42–9.69) mm in length by 4.07 ± 0.08 (range, 2.28–5.13) mm in width. The ovoidal cavities within these galls averaged 3.77 ± 0.08 (range, 2.28–4.84) mm in length by 2.13 ± 0.04 (range, 1.42–2.85) mm, not much larger than the mean size of the puparia reported above. The lack of feces or frass within the cell and small size of the gall supporting complete development of larvae of nearly equal size supports the assumption that the larval diet consists largely of liquid nutrients translocated to the gall—a foreshortened axillary branch or stem apex (Fig. 8G)—acting as what Harris and Shorthouse (1996) so eloquently have characterized, documented, and explained as a "plant nutrient sink."

Adult.—Under insectary conditions, 26 males (Fig. 8H) lived an average of 20 ± 2 (range, 4–40) days, and 28 females (Fig. 8I) an average of 17 ± 2 (range, 5–35) days.

Mating behavior.—The premating, mating, and postmating behaviors of *O. aterrima* were not studied in the field, but were observed in petri dish arenas of the type found to be so useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). In these arenas, adults exhibited behavior typical of other circumnatal, gallicolous species, cf., *Procecidochares,* previously studied in southern California, i.e., a lack of courtship behavior, the exhibition of enantion type of wing movements by both sexes, and male stalking of females prior to mating (Green et al. 1993, Goeden and Norrbom 2001, Headrick and Goeden 1994). Moreover, both sexes displayed rapid wing enantion and lofting during copulation, especially females, if agitated, just prior to postcopulatory separation.

Mating behavior of *O. aterrima* was similar to that reported for *Procecidochares kristineae* Goeden by Silverman and Goeden (1980) and Goeden and Teerink (1997) and *P. blanci* Goeden and Norrbom (2001). Males tracked females slowly and aggressively mounted them by jumping onto their dorsa usually from behind. Once mounted, males clasped the dorsolateral anterior margins of abdominal tergite 3 of the females with their foretarsal claws; the middle tarsi grasped the base of the oviscape laterally, and the hindtarsi rested on the substrate (Fig. 9A). The wings of the female were

Fig. 9. Mating pairs of *Oxyna aterrima:* (A) ventral view; (B) dorsal view; (C) lateral view on leaf. Lines = 1 mm.

parted at about 45° (Figs. 9A, B), those of the male at 30° (Figs. 9A, B), with both pairs of wings more or less centered over the midline of both flies. The mouthparts of a mounted male were held above the scutellum of a female. The oviscape of females in copula were elevated about 30° above the horizontal, with the rest of her body more or less parallel to the substrate; the body of the males was angled upward 30°.

Ten copulations (Figs. 9A, B, C) averaged 149 ± 30 (range, 28–330) minutes in duration and occurred throughout the day in bright sunlight, when the flies were most active. Males mounted females perfunctorily and aggressively initiated copulation, sometimes forcefully holding the females on the substrate. Prior to postcopulatory separation, females evidenced restlessness and attempted to dislodge males by arching the junction of the thorax and abdomen upward and by pushing against the male body with their hind tarsi. The wings of mounted females also were pushed upward against the mounted males at this time. Males responded with copulatory induction behavior (Headrick and Goeden 1994), which consisted of rubbing the underside of the oviscape with their hind tarsi in order to calm the female. Two instances of postcopulatory separation were noted in which the male rapidly dismounted from the female posteriorly and continued walking as his phallus was pulled free; two such uncouplings last 4 and 10 seconds.

Seasonal history.—*Oxyna aterrima* is a univoltine, circumnatal species (Headrick and Goeden 1994, 1998) on *A. tridentata* in southern California. Eggs are laid in axillary buds, terminal buds of axillary branches, or in terminal buds of stems in spring (May–June) and the young larvae pass the summer (June–September) as first instars. These larvae molt to the second instar and wait until early winter to molt to the third instar, the stage in which they overwinter. The third instars complete their development in early spring (March) of the following year at the time of the renewed flush of host-plant growth. Pupariation and adult emergence follow (April) and the short-lived adults mate and probably oviposit on or near the same plants from which they emerged.

Natural enemies.—Several individual *Mesopolobus* sp. and *Pteromalus* sp. (Hymenoptera: Pteromalidae) and a single individual of *Eupelmus* sp. (Hymenoptera: Eupelmidae) were reared from larvae or puparia of *O. aterrima* as solitary, larval and/or pupal ectoparasitoids. A sample of 33 galls collected at Mojave River Forks at 914-m elevation, SW San Bernardino Co., on 10.iv.1996, contained 10 empty puparia, remains of five, dead, parasitized, third instars, and 18 empty galls presumably opened by bird predators. Another sample of 80 galls collected West of Silverwood Lake at 1,066 m, San Bernardino National Forest, SW San Bernardino Co., on 10.iv.1996 contained 15 empty puparia, remains of five dead, parasitized third instars or puparia, and 60 empty galls presumably opened by birds. And, a sample of 39 galls collected at upper end of Horsethief Canyon at 1,140 m, San Bernardino National Forest, SW San Bernardino Co., on 10.iv.1996 contained 18 empty puparia, eight remains of parasitized third instars or puparia, and 13 empty galls presumably opened by birds. Bird predation by bushtits, *Psaltriparus* sp., on *Eutreta diana* (Osten Sacken) in galls on *A. tridentata* was reported by Goeden (1990).

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NOTE

First Record of Biting Midges (Diptera: Ceratopogonidae) Attacking Frogs in the Neotropical Region

The biting habits of females of the subgenus *Forcipomyia* (*Lasiohelea* Kieffer) Meigen on frogs are relatively well known in the northern hemisphere. *Forcipomyia velox* (Winnertz) has been reported to feed on the edible frog *Rana esculenta* Linnaeus in Europe (Desportes and Harant 1940; Desportes 1941, 1942). In China, *F. emeishana* (Yu and Liu) and *F. propria* Chan and LeRoux feed on *Bufo melanosticus* Schneider and *Rana plancyi* Lataste, respectively (Lien 1989). *Forcipomyia fairfaxensis* Wirth has been recorded feeding on *Rana catesbeiana* Shaw, *R. clamitans melanota* (Rafinesque), and unidentified frogs in Ontario, Canada (Pechuman and Wirth 1961, Gruia-Gray and Desser 1992, Marshall 1997). Feeding on frogs by ceratopogonids in the Neotropical Region was previously unknown.

During a series of studies of frog behavior in a small pond (about 25 m^2) situated in the surroundings of the city of Corrientes in northeastern Argentina (27°30′S, 58°45′W), one of us (EFS) observed a small cloud of midges, 4–8 cm in diameter, flying over individuals of two species of frogs, *Leptodactylus chaquensis* Cei and *Pseudis paradoxa* Gallardo. These two species of frogs behaved differently, while *L. chaquensis* was relatively inactive, with its head above the water for about 30 minutes, *P. paradoxa* did not keep its head above the water for more than 10 minutes.

The observations were made between February 14 and February 28, 2001. The clouds of midges were composed of about 20–30 females flying over the frogs from 3 pm to 8 pm every day, but stopping at night. When the clouds were present, 5–10 midges were also recorded directly on the frogs, where they landed on the snout and on the interorbital space. The two species of frogs reacted in a different way to the presence of the insects: *L. chaquensis* ignored them, whereas individuals of *P. paradoxa* exhibited signs of irritation, showing a series of movements when the clouds were located 1 or 2 cm above them. The observers assumed that the flies were biting the frogs, at least *P. paradoxa,* although this was not directly confirmed.

Although the observers (EFS and AIK) were located as close as 1 m from the flying clouds of females, the midges did not attack them. Approximately 20 midges were collected using an entomological net, and identified by GRS as belonging to the subgenus *Forcipomyia* (*Lasiohelea*) (Diptera: Ceratopogonidae). They most likely belong to an undescribed species, but because males typically provide better taxonomic features in this subgenus, this species of *Forcipomyia* is best left unnamed for the present.

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Gustavo R. Spinelli, *Departamento Científico de Entomología, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina* (e-mail: spinelli@museo.fcnym.unip.edu.ar); Eduardo F. Schaefer and Arturo I. Kehr, *Centro de Ecología Aplicada del Litoral (CECOAL-CONICET), Casilla de Correo 140, 3400 Corrientes, Argentina.*

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BOOK REVIEW

Terrestrial Heteropterans: A Field Guide to Japanese Bugs II. T. Yasunaga, M. Takai, and T. Kawasawa, eds. Zenkoku Noson Kyoiku Kyokai Publishing Co., Tokyo [in Japanese]. 2001. 350 pp. ISBN 4-88137-089-8 C3645. 9500 JPY (U.S. ca. $90).

Japan's rich tradition in natural history benefits from a cadre of amateur entomologists. School children carrying insect nets is a familiar sight. Contributions to the knowledge of Japan's true bugs (Hemiptera-Heteroptera) continue to be made by both amateur and professional entomologists.

The most recent faunal work on the terrestrial Heteroptera of Japan is *A Field Guide to Japanese Bugs II,* edited by Tomohide Yasunaga, Mikio Takai, and Tetsuo Kawasawa. The last-named editor was instrumental in publishing the first major faunal guide to Japanese bugs (Kawasawa and Kawamura 1975). Volume 1 of the current series of field guides (Yasunaga et al. 1993) treated 352 species of terrestrial heteropterans, representing 22 families of the infraorders Cimicomorpha and Pentatomomorpha; its 144 excellent color plates contain 740 images. Because the Japanese true bug fauna includes at least 800 species, revisions to the popular 1993 field guide were needed. Thus, volume 2, covering the Microphysidae, Miridae, Anthocoridae, and Cimicidae was issued in 2001.

Chapter 1 outlines the higher classification of the Japanese fauna of true bugs. The infraorders and superfamilies follow those used in the *Catalogue of the Heteroptera of the Palaearctic Region* (Aukema and Rieger 1995).

The heart of the book is Chapter 2, which treats the Japanese Cimicomorpha: Microphysidae (1 species) and Miridae (404 species) in the Miroidea, and Anthocoridae (40 species) and Cimicidae (2 species) in the Cimicoidea (deferred until Volume 3 are the remaining cimicomorphs—tingids, nabids, and reduviids plus 18 families in the Pentatomomorpha). Occupying the first 96 pages of this chapter are the color plates. Nearly all the approximately 800 images are of excellent quality, and many are among the most lifelike and stunning I have seen of heteropterans. Except for three plates of adults mounted on points, the bugs—adults and sometimes nymphs—appear on their host plants. Symptoms of mirid feeding are shown in two plates. Pages 111-307 contain descriptions (mostly by Yasunaga, with Deraeocorinae by Nakatani and Yasunaga) of the various species. A key to the eight subfamilies of Miridae is included. Also included are 31 line illustrations and 27 boxes or columns with additional information.

In Chapter 3, Takai and Yasunaga briefly discuss the economically important mirids, both plant pests and predators. Chapter 4 consists of Yasunaga's discussion of dissecting and interpreting the male genitalia of mirids and anthocorids. The book concludes with references (42 titles), glossary, and index to genera and species.

This field guide to the terrestrial Heteroptera of Japan is indispensable for those who conduct research on Japanese bugs, or for anyone in Japan who wants to observe or identify bugs. The book, even though written in Japanese, is useful for North American heteropterists; merely having the exquisite color plates at hand is sufficient justification for purchasing the book. In an age of increasing globalization and cosmopolitanization of biotas, this excellent field guide also should be acquired by major museums and university libraries in North America, as well as by regulatory agencies involved with plant protection.

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104(2), 2002, pp. 529–531

BOOK REVIEW

Biology of the Plant Bugs (Hemiptera: Miridae). Pests, Predators, Opportunists. By Alfred G. Wheeler, Jr. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, 507 pp. 2001. Cost: $95.00 (cloth).

Uncommonly outstanding books in science come along only once in awhile. Al Wheeler's *Biology of the Plant Bugs* belongs among the better works of its kind to appear in many years. This book begins with a foreword by Sir Richard Southwood, well-known ecologist, heteropterist, and coauthor of the now classic *Land and Water Bugs of the British Isles.* The 507-page *Biology of the Plant Bugs* is separated into five parts and 18 chapters, three appendices, a glossary, references cited, and two indices, one on animal names and one on subject matter.

Part I, titled "Background," is comprised of four chapters. Wheeler introduces plant bugs as underappreciated insects, compared with beetles, dragonflies, and butterflies, and gives many reasons why they deserve more attention. A rather lengthy mirid primer (table 1.1) provides a good overview of mirid characteristics. What characters define the Miridae? How long is the largest plant bug? Nymphs go through how many instars? These are just a few of the facts found in this primer. Wheeler also gives a thorough review of the terminology he follows, from the differences between "injury" and "damage" to the use of "nymph" rather than "larva" for hemimetabolous immatures. The classification of the Miridae used in this book generally follows that of Schuh's world catalog (1995. Plant Bugs of the World. New York Entomological Society, New York. 1329 pp.), but Wheeler offers corrections he has detected or that have been pointed out by others. Users should also consult Kerzhner and Josifov's Palearctic catalog (1999. Miridae, pp. 1–577. In: Aukema, A. and C. Rieger [eds.]. Catalogue of the Heteroptera of the Palaearctic Region, The Netherlands Entomological Society, Amsterdam) and Kerzhner and Schuh's paper (2001. Journal of the New York Entomological Society 109: 263–299) on corrections and additions to the Schuh catalog.

Part II, covering "Perspectives," is separated into three chapters. Wheeler provides a review of family characteristics and aids needed for the identification of Miridae that rivals most systematics works in its thoroughness and technical accuracy. It is filled with numerous adult habitus drawings depicting examples of all subfamilies and representative tribes. These are accompanied by many figures illustrating important mirid attributes, including diagnostic pretarsal structures, types of vestiture, male and female genitalia, and egg morphology. The remainder of this part presents many interesting facts on mirid diversity, ecology, and behavior. Despite the apparent "delicate" makeup of Miridae, you will learn about a mirid that holds the world altitude record for a heteropteran. There are details on habitat preferences, including some quite unusual ground-inhabiting species or those specializing in rare plants. How do mirids disperse? Several sections on wing polymorphism offer interesting insight into the "trivial" flight patterns of plant bugs and how this affects their capability to disperse. There are also extensive discussions on sex pheromones, acoustical communication, reproductive behavior, oviposition, fecundity, longevity, nymphal feeding, and much more. Wheeler successfully brings together an informative discussion on mouthpart morphology and feeding strategies, giving such details as how mirid feeding differs from other hemipterans and facts on endosymbionts in the gut, host selection, extra-oral digestion, and salivary secretions. How important are mirids as vectors of viruses and other plant pathogens? You will want to read Chapter 7 to find out.

Part III begins what might be considered the "backbone" of the book with a look at phytophagy. Rather than looking at specific plant bugs and their feeding habits, Wheeler has elected to examine the parts of plant that are attacked and the diverse array of mirids that feed on them. The five chapters in this part of the book examine the symptoms—apparent or unapparent—on various plant parts. We learn that not all leaf and stem feeders cause injury that produces visible symptoms. In such cases, considerable physiological stress still may be exerted, resulting in yellowing, wilting, growth retardation, and reduction in yields. Leaf crinkling, shot holing, silvertop, lesions, and cankers also are among the many topics you will find discussed in great detail. Why are some flowering structures more attractive to insects than others? How do mirids affect cotton? Want to learn more about nectar and pollen-feeding or mirid pollinators? An entire chapter (Chapter 11) is devoted to such specialists. What mirids attack apple, avocado, cocoa, and olive? What is the economic threshhold of *Lygus lineolaris* (Palisot de Beauvois) on apple? Part III provides the most thorough review of plant-feeding mirids I have seen. If you do not find the answer about a particular plant bug here, it is a good bet that nothing has been published.

Part IV makes a major shift to mirid predators. Despite the common name plant bug, a surprising number of mirids are zoophagous. What percentage of Miridae rely on animal matter in their diets? You may be surprised at the answer. Predatory mirids may be characterized as zoophytophages, phytozoophages, or simply zoophages. Where do facultative predators fit in? Are mirids specialists or generalists? What kinds of prey are preferred? You will find answers to these and many other questions in the two chapters covering zoophagy.

Wheeler provides a synthesis of all of the previous chapters in Part V. He offers a discussion of the work that speculates on ancestral feeding habits of the Miridae. Were they phytophagous or zoophagous? What are the feeding trends among the higher mirid groups? What would an eccritotarsine do when offered a tasty caterpillar? Find out what feeding specializations have evolved in the Termatophylini. Figure 17.1 offers a novel perspective of the feeding habits plotted across subfamilies based on phylogenetic relationships. The last chapter brings to a close the *Biology of the Plant Bugs* with a summary of what we know and what we do not know about mirids. Here Wheeler takes a final look at the various feeding modes and habits and offers his parting thoughts.

This book is profusely illustrated. The quality of figures ranges from good to outstanding. Virtually all line drawings and graphs are borrowed from the literature, but they are carefully selected and provide good support for the text. A bonus not often found in scientific works is 24 beautiful full-color plates, providing many examples of adults and nymphs, eggs and oviposition scars, mirid predators and parasitoids, and a wide array of the kinds of damage caused by mirids.

I know a good book review is supposed to contain criticism as well as praise, but it has proved difficult to find anything substantially negative about this volume. A better literature review? The bibliography, containing more than 5,000 citations (135 pages!), surpasses the largest taxonomic catalogs, a fact I think anyone will find amazing. I am not a strong proponent of tables to summarize repetitive data. In this book, Wheeler uses tables extensively, but he does so effectively. They are concise, well-organized, easy-to-follow, and provide information on many poorly known, more obscure taxa.

As Sir Richard Southwood writes in his foreword, this is a book for all organismal biologists, agricultural workers, and specialists of biological control. If you are interested in insect biology, particularly that of the Heteroptera, you are going to want this book on your shelf. There is no doubt that it will stimulate considerable biological research on Miridae for many years to come, placing it at a lofty level with Butler's (1923) "*Biology of the British Hemiptera-Heteroptera*" and Kullenberg's (1944) "*. . . Biologie der Capsidae.*"

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REPORTS OF OFFICERS

EDITOR

Volume 103 of the *Proceedings* included four issues with a total of 1,044 pages. Eighty-eight regular papers, five notes, eight book reviews, Society Meetings, Reports of Officers, and the Table of Contents for Volume 103 were published. The number of different authors in this volume totaled 144. About 105 manuscripts were submitted for consideration for publication during the past year (Nov. 1, 2000 to Oct. 31, 2001).

Two *Miscellaneous Publications* are in preparation: "A revision of the Oriental species of *Aphthona* Chevrolat (Coleoptera: Chrysomelidae)" by Alexander S. Konstantinov and Steven W. Lingafelter and "Revision of the genus *Anoplophora* (Coleoptera: Cerambycidae)" by Steven W. Lingafelter and E. Richard Hobeke (the genus that includes the Asian longhorned beetle). One *Memoir* is also in preparation, "Holcocerini of Costa Rica (Lepidoptera: Gelechioidea: Coleophoridae: Blastobasinae)" by David Adamski. All are expected to be published in 2002.

I extend thanks to Ray Gagné, *Book Review Editor,* for excellent work in obtaining book reviews for the *Proceedings,* and to Wayne Mathis and Tom Henry of the Publications Committee for their continued advice and support. Marie Blair and Cathy Anderson provided much needed assistance in handling correspondence, routing manuscripts, and preparation of manuscripts and plates for the printer.

I am also grateful to the many reviewers for their time-consuming efforts and constructive reviews of manuscripts. Their contributions are essential to help increase the quality of papers published in the *Proceedings.*

Respectfully submitted,
David R. Smith, *Editor*

TREASURER

SUMMARY FINANCIAL STATEMENT FOR 2001

	General Fund	Special Publication Fund	Total Assets
Assets: November 1, 2000	$36,862.01	$143,034.86	$179,896.87
Total Receipts for 2001	$89,981.67	$35,780.74	$144,219.60
Total Disbursements for 2001	$90,739.86	$5,910.75	$96,650.61
Assets: October 31, 2001	$36,103.82	$172,904.85	$209,008.67
Net Changes in Funds	$(758.19)	$29,869.99	$29,111.80

Audited by the Auditing Committee, December 3, 2001 consisting of Norman E. Woodley, Chairman, Steven W. Lingafelter, and Thomas J. Henry. Presented to the membership at the meeting of December 6, 2001.

Respectfully submitted,
Michael G. Pogue, *Treasurer*

Membership

In 2001 the Society received applications for new membership for 18 people as follows:

Vladimir V. Baicher
Matthew L. Buffington
Federico C. Ocampo
M. S. Roberto Arce-Perez
John Franclemont
Dan Kjar
Charyn Micheli
Jonathan Mawdsley
Paul A. Opler
Wendell Pennington
Oscar G. Pérez
Vyvy N. Pham
Michael Philip
Jonathan Polloni
Gordon F. Pratt
Robert E. Roughley
John Strazanac
Terry Wheeler

Each applicant was sent a letter acknowledging receipt of his/her application, and his/her name was read at a regular meeting of the Society and repeated in the minutes of the following meeting. The number of applications is down 22% from 2000.

Respectfully submitted,
Steven W. Lingafelter,
Membership Chair

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SOCIETY MEETINGS

1,057th Regular Meeting—June 28, 2001

The 1,057th meeting of the Entomological Society of Washington (ESW) convened at 7:00 p.m. at the Uniformed Services University of Health Sciences in Bethesda, Maryland and consisted of the annual banquet, which was held jointly with the Maryland Entomological Society. About 100 people attended. Gabriela Chavarria was Mistress of Ceremonies, a title she graciously elaborated upon. The guest speaker was Dr. Quentin Wheeler, professor at Cornell University and director of the systematic biology program at the National Science Foundation. Dr. Wheeler wore both hats for his presentation "Return to the Little-known Planet." As the director of an NSF branch, he was pleased with the quality of systematic proposals and successes by funded research. As a professor at Cornell, however, he lamented the continuing decline in numbers of systematists trained in morphology. Synthesizing both aspects, Dr. Wheeler closed by discussing the challenges and opportunities facing all modern systematists.

The meeting was adjourned at approximately 8:45 p.m.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,058th Regular Meeting—October 4, 2001

The 1,058th regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room (CE-340) of the National Museum of Natural History, Washington, D.C., by President John Brown at 7:10 p.m. The meeting was attended by 11 members and 4 guests. The minutes of the 1056th and 1057th meetings were approved as read.

Membership Chair Steve Lingafelter read the names of five new applicants for membership: Wendell Pennington, Terry Wheeler, Frederico Ocampo, Vladimir Baicher, and M. S. Roberto Arce-Perez; Vladimir introduced himself.

For exhibits, Arthur Evans showed slides of summer beetles and a few token leps, mostly from the Western United States. Dave Furth showed slides of NHB East Wing renovations for Smithsonian Entomology that are now complete. Warren Steiner exhibited a book, "*Vista Nieve*" by M. R. Carriker, which gives a good account of collecting expeditions in Colombia in the late 1800's. Edd Barrows passed around some live, local forest insects in petri dishes.

New Program Chair Ron Ochoa introduced William P. Wergin, director of the USDA Agricultural Research Service Electron Microscopic Unit, who spoke about "Low Temperature Scanning Electron Microscopy and its Application for Studies of Soft-bodied Arthropods." While scanning electron microscopy (SEM) has been around for about 30 years, its use for biological specimens, which are typically 10%–50% water, has always involved some artifacts, principally distortion with dehydration and loss of fine detail. Even low-temperature SEM began in the 1970's, but with its own limitations, e.g., reduced specimen mobility. Up to 10 years ago, 400× was about the maximum magnification one could use to generate publishable micrographs. Dr. Wergin's lab has refined the low-temperature SEM using Field Emission SEM and pushed the limits, able to see even cell membrane particles (10 nanometers), and commonly work in the range of 100,000 to 200,000× magnification. Specimens are dipped in liquid nitrogen and scanned without coating. This method is particularly well suited for 'unfixable' tissues (e.g., internal features of nematode eggs), soluble materials (e.g., snowflakes), delicate tissues, physiologically active tissues (e.g., live muscle contractions of nematode 'faces'), or loosely attached tissues. A notable application was in examining scolytid beetles covered with a mite species that was being considered for mass release for biological control. The low-temperature SEM's 'frozen-in-action' images revealed that the mites were feeding not on the beetle but rather on beetle-parasitic nematodes, of which the researchers had been totally unaware. In summary, low-temperature SEM allows visualization of hydrated tissue, free of artifacts and therefore has widespread application in entomology (and acarology).

The meeting was adjourned at 8:37 p.m. Refreshments were provided by Ron Ochoa and John Brown.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

1,059th Regular Meeting—November 1, 2001

Undaunted by the potential threat of terrorist activities, undeterred by increased museum security, and unimpressed by the looming Game 5 of the World Series, attendees of the 1,059th regular meeting of the Entomological Society of Washington settled into their seats in the Cathy Kerby room of the National Museum of Natural History at 7:08 p.m. when the meeting was called to order. In attendance were 13 stalwart members and 3 fearless guests. The minutes of the 1,058th meeting were ably read by Jill Swearingen (volunteer minute-reader) and were approved with little modification.

Membership Chair Steve Lingafelter read the names of two new applicants for membership: Jonathan Polloni and Charyn Micheli. Steve introduced Charyn, who is a new graduate student in the MCSE program and will be studying Cerambycidae. Art Evans shared a CD of cricket and katydid songs, a book on scarab beetles, and a meeting announcement. Wayne Wehling told us of a new federal law regarding the interstate commerce of live insects. The action is currently in the 60-day "review and comment period." Vladimir Baicher shared cells of a nest of a local wasp. And last, but of course, not least, David Furth shared a book.

John Brown (pinch-hitting for Ron Ochoa) introduced Dr. Rebecca (alias Becky) Simmons, whose talk was entitled "The Evolution of Wasp Mimicry in Euchromiine Tiger Moths (Arctiidae: Euchromiinae)." At the heart of Becky's presentation were an analysis of the phylogenetic patterns of mimicry within Euchromiini and a test to determine whether these patterns conform with the recently proposed model of Quasi-Muellerian Mimicry. To Becky's surprise, they do not. Becky's study concluded that nuances of predator behavior, not prey degree of palatability, more likely drives the evolutionary process of mimicry in this group.

The meeting was adjourned at about 8:15 p.m. Refreshments were provided by your society.

Irreverently submitted,
John W. Brown

1,060th Regular Meeting—December 6, 2001

The 1,060th regular meeting of the Entomological Society of Washington (ESW) was called to order in the Cathy Kerby room of the National Museum of Natural History, Washington, D.C., by President John Brown at 7:08 p.m. The meeting was attended by 20 members and 3 guests. The minutes of the 1,059th meeting were approved as read.

David Smith, Editor, summarized another impressive year of the *Proceedings,* with about 105 manuscripts submitted for consideration, over 1,000 pages published, and two *Miscellaneous Publications* in preparation. Membership Chair Steve Lingafelter noted that we had only 18 new members this year, down 22% from last year. There were no new applicants for membership at this meeting. The end-of-year audit committee, chaired by Norm Woodley, reported a whopping $209,008 in total assets, the great majority in the special publication fund.

Two visitors were introduced. In miscellaneous business, elections were held. Because no slate of officers had been proposed at the November meeting, David Furth afterwards rounded up volunteers and shared the list with 20 active members. At this meeting, the slate was passed unanimously as follows: President Elect: Jon Mawdsley; Editor: David Smith; Program Chair: Ron Ochoa; Membership Chair: Steve Lingafelter; Corresponding Secretary: Holly Williams; Custodian: Jon "Buck" Lewis; Treasurer: Michael Pogue; and Recording Secretary: Stuart McKamey.

For exhibits, Ollie Flint shared some rare caddisfly specimens endemic to springs in the Smokies. Gabriela Chaverria shared the book "*Insects and Gardens,*" by ESW member Eric Grissell. Dave Furth displayed several recent books: "*Dragonflies of Sri Lanka*" by T. de Fonseca; "*Forensic Entomology: The Utility of Arthropods in Legal Investigations,*" which is a textbook style reference edited by J. H. Byrd and J. L. Castner; and "*Guide to the Butterflies of Russia and Adjacent Territories, Volume 2*" (Pensoft Publishers, Moscow). Dave also shared a mystery wooden box received from Nigeria, loaded with beetle exit holes and contents still unknown, pending further freezer treatment.

Ron Ochoa introduced the evening's speaker, Arthur Evans, Smithsonian Research Associate and author of popular entomology literature. His talk was entitled "Sky Islands, Desert Sea—a Field Guide to the Arthropods of Southern Arizona." True to the title, Art presented slides that may in the future end up in a field guide he is preparing for the region, covering a wide range of myriapods, arachnids, and insects. Most slides were accompanied by life history notes, many of which included rearing methods garnered from his experience as director of the Insect Zoo at the Los Angeles County Museum.

The meeting was adjourned around 8:30 p.m. Refreshments were provided by the Society.

Respectfully submitted,
Stuart H. McKamey,
Recording Secretary

PUBLICATIONS FOR SALE BY THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

MISCELLANEOUS PUBLICATIONS

A Handbook of the Families of Nearctic Chalcidoidea (Hymenoptera), by E. Eric Grissell and Michael E. Schauff. 85 pp. 1990	$10.00
A Handbook of the Families of Nearctic Chalcidoidea (Hymenoptera): Second Edition, Revised, by E. Eric Grissell and Michael E. Schauff. 87 pp. 1997	15.00

MEMOIRS OF THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

Memoirs 2, 3, 7, 9, 10, 11, and 13 are no longer available.

No. 1.	The North American Bees of the Genus *Osmia,* by Grace Sandhouse. 167 pp. 1939	$15.00
No. 4.	A Manual of the Chiggers, by G. W. Wharton and H. S. Fuller. 185 pp. 1952	15.00
No. 5.	A Classification of the Siphonaptera of South America, by Phyllis T. Johnson. 298 pp. 1957	15.00
No. 6.	The Female Tabanidae of Japan, Korea and Manchuria, by Wallace P. Murdoch and Hirosi Takahasi. 230 pp. 1969	15.00
No. 8.	The North American Predaceous Midges of the Genus *Palpomyia* Meigen (Diptera: Ceratopogonidae), by W. L. Grogan, Jr. and W. W. Wirth. 125 pp. 1979	12.00
No. 12.	The Holarctic Genera of Mymaridae (Hymenoptera: Chalcidoidae), by Michael E. Schauff. 67 pp. 1984	5.00
No. 14.	Biology and Phylogeny of Curculionoidea, edited by R. S. Anderson and C. H. C. Lyal. 174 pp. 1995	25.00
No. 15.	A Revision of the Genus *Ceratopogon* Meigen (Diptera: Ceratopogonidae), by A. Borkent and W. L. Grogan, Jr. 198 pp. 1995	25.00
No. 16.	The Genera of Beridinae (Diptera: Stratiomyidae), by Norman E. Woodley. 231 pp. 1995	25.00
No. 17.	Contributions on Hymenoptera and Associated Insects, Dedicated to Karl V. Krombein, edited by B. B. Norden and A. S. Menke. 216 pp. 1996	25.00
No. 18.	Contributions on Diptera, Dedicated to Willis W. Wirth, edited by Wayne N. Mathis and William L. Grogan, Jr. 297 pp. 1997	25.00
No. 19.	Monograph of the Stilt Bugs, or Berytidae (Heteroptera), of the Western Hemisphere, by Thomas J. Henry. 149 pp. 1997	18.00
No. 20.	The Genera of Elaphidiini Thomson 1864 (Coleoptera: Cerambycidae), by Steven W. Lingafelter. 118 pp. 1998	12.00
No. 21.	New World *Blepharida* Chevrolat 1836 (Coleoptera: Chrysomelidae: Alticinae), by David G. Furth. 110 pp. 1998	12.00
No. 22.	Systematics of the North American Species of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae), by John D. Pinto. 287 pp. 1999	28.00
No. 23.	Revision of the Net-Winged Midges of the Genus *Blephariceria* Macquart (Diptera: Blephariceridae) of Eastern North America, by Gregory W. Courtney. 99 pp. 2000	14.00

Back issues of the Proceedings of the Entomological Society of Washington are available at $60.00 per volume to non-members and $25.00 per volume to members of the Society.

Prices quoted are U.S. currency. Postage extra except on prepaid orders. Dealers are allowed a discount of 10 percent on all items, including annual subscriptions, that are paid in advance. All orders should be placed with the Treasurer, Entomological Society of Washington, ℅ Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0168.

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NOTE

BOOK REVIEWS

MISCELLANEOUS